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VOLUME 19 SEPTEMBER, 1945 NUMBER 5

REVIEW OF LATEST PALEOCENE AND EARLY EOCENE MAMMALIAN FAUNAS

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ABSTRACT—All the latest Paleocene (Clarkforkian) and the Early Eocene (Wasatchian) mammalian remains discovered in North America are from Rocky Mountain intermontane basins. The composition and correlation of each collection, or fauna, is herein briefly discussed. A list of the known Clarkforkian and Wasatchian species supplies the data for detailed analyses. The three successive Early Eocene faunas, from the superposed Gray Bull, Lysite, and Lost Cabin beds, have been selected as diagnostic of early, middle, and late Wasatchian respectively. The beginning of the Eocene epoch is marked by the first appearance of 12 families, evincing the most significant faunal change since the Middle Paleocene. So similar a new fauna appeared at the same time in Europe that a migration is postulated. Genera that began later in the Eocene were largely the result of diversification of the new Early Eocene families. During early Cenozoic time a warm-temperate climate prevailed in the heavily wooded lowlands in the Rocky Mountain basins. However, the increased number of ungulate mammals in the Early Eocene indicates a gradual extension of grasslands, a process which continued throughout later Cenozoic time. Among Wasatchian fossils two faunal facies are represented. One, composed chiefly of diminutive multituberculates, marsupials, insectivores, primates, and rodents, was an arboreal forest facies. The other inhabited the savannahs and was composed mainly of larger terrestrial mammals—"subungulates," condylarths, creodonts, artiodactyls, and perissodactyls.

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INTRODUCTION AND ACKNOWLEDGMENTS

Most of the early Cenozoic continental deposits of North America and many mammalian fossils preserved in them were discovered by members of the United States government surveys of the West. As early as 1859 Hayden had noted Early Eocene strata in the Wind River Basin, Wyoming. Both Cope and Marsh found a few fragmentary fossils east of Evanston and in the vicinity of Black Buttes, Wyoming, in 1872–73, but the first large Early Eocene assemblage was secured by Cope in 1874 in the San Juan Basin, New Mexico. A year later Marsh also collected from this locality. In 1880 Wortman, directing Cope's field party, prospected in the Wind River Basin and recovered many valuable specimens. He visited the Big Horn Basin, Wyoming, the following year and there he found the richest Early Eocene fauna. Cope's great memoir of 1884, "The Vertebrata of the Tertiary formations of the West," climaxed this epoch of exploration.

Further collecting from these areas, particularly by Wortman and Granger under the auspices of the American Museum of Natural History, and by Loomis of Amherst, and Sinclair and Jepsen of Princeton, augmented the Early Eocene assemblage so that now it is one of the best-known Cenozoic faunas. Although most of the fossil material is fragmentary, species of 11 genera are represented by complete skeletons and species of seven more genera by partial skeletons.

All the Early Eocene mammalian fossils are from Rocky Mountain intermontane basins (fig. 1); none has been discovered elsewhere. As a consequence mammals that roamed over other parts of the continent in Early Eocene time remain unknown.

The most comprehensive revision of the fauna was made by Matthew and Granger. This work, together with studies of various biologic groups by Denison, Jepsen, Loomis, Osborn, Simpson, and Sinclair, serves as the principal source of paleontologic information in the present review. Unless specially noted the genera and species are catalogued by Hay (1902, 1930), Camp and Vanderhoof (1940), and Camp, Taylor, and Welles (1943); hence no references to original descriptions are cited.

These data have been compiled because the extensive literature on the Early Eocene fauna includes no detailed summary or synthesis of its composition. The material is arranged so as to be useful in identifying latest Paleocene and Early Eocene mammals and interpreting their ecologic relationships, and in correlating early Cenozoic stratigraphic units. Moreover, information concerning the primitive and modern aspects of the Early Eocene fauna disclosed by the splendid Late Paleocene collections recently discovered and described, has been incorporated into the conclusions.

The accompanying references are not exhaustive. Only the more pertinent papers are cited, but through them a complete bibliography is available.

To Dr. G. L. Jepsen, I am indebted for many suggestions regarding Paleocene and Eocene mammalian faunas, and for his helpful advice during the preparation of this paper. I am grateful to Dr. J. B. Knight for constructive criticism of the manuscript, and to Dr. E. H. Colbert for use of the facilities of the American Museum of

FIG. 1—Sketch map of Rocky Mountain intermontane basins.

TENTATIVE CORRELATION OF LATE PALEOCENE AND EARLY EOCENE MAMMALIAN FAUNAS

Epoch	Age	Powder River Basin	Big Horn Basin	Wind River Basin	Bridger Basin	Washakie Basin	Laramie Basin	Uinta Basin	Piceance Creek Basin	Huerfano Basin	San Juan Basin	European Age
Early Eocene	Wasatchian late	?[1]	Lost Cabin	Lost Cabin	LaBarge	? Dad ?	? Cooper Creek ?	Not named	Not named	Huerfano A	----------	Cuisian
	Wasatchian middle		Lysite	Lysite		?		?			Largo	
	Wasatchian early		Gray Bull	Not named					?		Almagre	---------- Sparnacian
Late Paleocene	Clarkforkian		Clark Fork									Thanetian
	Tiffanian		Silver Coulee						Plateau Valley		Tiffany	

[1] ? indicates that Early Eocene fossils are known but their correlation is uncertain.

Natural History. Important data were generously supplied by Drs. R. H. Denison, G. G. Simpson, H. E. Wood, II, Messrs. Bryan Patterson and J. L. Kay.

DESCRIPTIVE INDEX OF CLARKFORKIAN AND WASATCHIAN FAUNAS

General Statement

In this discussion collections of identifiable mammal remains from different localities or stratigraphic levels are called faunas even though they do not represent the totality of mammals that lived in the area. Usually each assemblage includes only those members of the "real fauna" most likely to be preserved. (See Simpson, 1937a, pp. 67–69.) If the fossils are few and from a small area the term local fauna is perhaps preferable.

Faunas that occur in superposed strata constitute a standard sequence, for their relative ages are definitely established. Other collections from isolated areas and incomplete sections can be fitted into a time scale according to their relationship to the standard sequence. The North American provincial ages Clarkforkian, Wasatchian, and Bridgerian, equivalent to latest Paleocene, Early Eocene, and Middle Eocene respectively, are based on such successive mammalian faunas (Wood *et al.*, 1941, pp. 1–10). The accompanying correlation table of the Late Paleocene and Early Eocene assemblages is founded principally upon the conclusions of the papers consulted. Geographic names in the table have been given to the faunas and the "patches" of rock in which the remains are preserved in order to distinguish them from the formations (or other lithogenetic units) in which they occur. It is important that this distinction in nomenclature be made because the fossiliferous rocks are not necessarily stratigraphically coextensive with the lithogenetic units containing them. A fossil assemblage may be found in more than one formation or only in a portion of a formation. The merits of this method of designating mammalian faunas and the particular beds in which they are preserved, as opposed to defining faunal zones, have been discussed by Stirton (1936, pp. 161–166), Jepsen (1940, pp. 223–235), Wood *et al.* (1941, pp. 5–8), and Van Houten (1944, pp. 172–177).

The names of species and subspecies listed in this paper have been taken from the literature. Inasmuch as the taxonomy of many of the biologic groups needs revision by modern methods all conclusions based on lists of species must be used cautiously. Most of the generic assignments are better established. Consequently the accompanying analyses are based on generic lists.

Future discoveries undoubtedly will modify current knowledge of the temporal ranges of many early Cenozoic mammals. Nevertheless it seems unlikely that the conclusions regarding the general relationships of the faunas discussed will be in error on that account.

Among the Early Eocene collections those from Gray Bull, Lysite, and Lost Cabin beds are the largest, and their stratigraphic relationships are well established. Therefore they have been selected as the diagnostic early, middle, and late Wasatchian faunas.

Clark Fork Fauna

Sinclair and Granger, 1912, pp. 59–60.
Granger, 1914, pp. 203–205.
Jepsen, 1930b, pp. 491–493.
Simpson, 1937b, pp. 1–24.
Jepson, 1940, pp. 237–238.

The Clark Fork fauna (table IV) has been recovered from the uppermost 500 feet of the Polecat Bench formation and locally from basal beds of the overlying Willwood formation (Van Houten, 1944, pp. 185–186) north of the Shoshone-Clark Fork divide in the northern part of the Big Horn Basin. Clark Fork beds are exposed in the Big and Little Sand Coulee drainages west of Polecat Bench, between Little Rocky Creek and Line Creek, and on the rugged southeast slope of Polecat Bench north of Powell. A few specimens have also been found in drab Polecat Bench deposits on the southwest flank of McCulloch Peaks.

Clarkforkian age, the latest Paleocene temporal unit, is based on this assemblage (tables I, II). The only genus restricted to the fauna is *Dipsalodon*, an oxyaenid creodont. (Patterson reports *Dipsalodon?* from Plateau Valley beds in northwestern Colorado.)

The following species and subspecies have been found only in Clark Fork beds:
Plesiadapis dubius
Palaeanodon parvulus
Esthonyx latidens (?Gray Bull also)
Dipsalodon matthewi
Oxyaena platypa
Oxyaena aequidens
Dissacus praenuntius
Didymictis protenus proteus
Ectocion parvus
Ectocion osbornianus ralstonensis
Coryphodon sp. nov.
Probathyopsis praecursor (?Gray Bull also)
Probathyopsis sp. nov.
Meniscotherium? priscum

The Clark Fork, like most Early Eocene assemblages, is composed chiefly of larger terrestrial mammals whose remains were preserved in flood plain deposits (see Simpson, 1937a, pp. 62–63). On the contrary, members of the somewhat older Paleocene faunas of Tiffanian age, the Tiffany, Bear Creek, Silver Coulee, and Melville, represent a forest facies and probably were mainly arboreal. An exception is the Tiffanian Plateau Valley assemblage, a terrestrial faunal facies, which, like the Clark Fork, includes primitive ungulates and creodonts. Because of this facies difference the Paleocene aspect of the Clark Fork fauna is obscured when compared with the Tiffanian arboreal faunas and, conversely, its Early Eocene characteristics are exaggerated. If, however, genera represented in both Tiffanian and Wasatchian collections are inferred to have lived during Clarkforkian time (but were members of an arboreal forest facies not yet discovered), then the Paleocene aspect of the Clarkforkian fauna becomes readily apparent (table I). Eight additional genera are thus suspected to have been Clarkforkian mammals: *Neoliotomus*, *Prochetodon*, *Ectypodus*, *Diacodon*, *Palaeosinopa*, *Phenacolemur*, *Chriacus*, and *Phenacodaptes*.

The augmented Clarkforkian fauna now contains 25 genera; 18 are from older assemblages, seven appear first in the Clark Fork. In the former category one genus, *Dipsalodon*, is not known above the Clark Fork, 10 genera are Gray Bull forms of Paleocene aspect not yet found above the Gray Bull (or Almagre), and seven are long-ranged Wasatchian genera from the Paleocene. Two of the seven genera beginning in the Clark Fork fauna occur only in the Gray Bull (or Almagre?). The other five that

first appear in the Clark Fork continue into the Lysite and Lost Cabin.

Gray Bull Fauna

Sinclair and Granger, 1911, pp. 107–108.
Sinclair and Granger, 1912, pp. 58–59.
Granger, 1914, pp. 203–205.
Jepsen, 1930a, pp. 117–119.
Jepsen, 1930b, pp. 493–496.
Van Houten, 1944, pp. 178–188.

The early Wasatchian Gray Bull fauna (table IV) is preserved in the red-banded Willwood formation in the Big Horn Basin. In variety of fossil mammals it is the richest of all the Early Eocene assemblages.

Almost every outcrop of the lower Willwood strata yields some Gray Bull fossils, but most of the specimens have been obtained from the northern badland slopes of McCulloch Peaks and in the vast badland tract west of the Big Horn River and south of the Greybull River, particularly in the Dorsey Creek and Elk Creek drainages.

By definition Gray Bull beds are delimited by the presence of *Homogalax*, a primitive tapirlike perissodactyl, which is known to occur through about 2000 feet of Willwood deposits. Granger (1914, p. 205) called the lowest 200 feet Sand Coulee beds, but Jepsen (1930b, p. 119) redefined the Gray Bull "to include the 'Sand Coulee beds,' inasmuch as the genus *Homogalax*, whose supposed absence from the latter was the basis of distinction, has been found in typical 'Sand Coulee beds.'" Delimitation of the Gray Bull by the presence of *Homogalax* is consistent with the use of perissodactyls as index fossils throughout the Eocene. However, in contrast to the 2000 feet thus assigned to the Gray Bull, most early Cenozoic faunas are restricted to fossiliferous beds 300 to 600 feet thick (Osborn, 1929, p. 56). This discrepancy in thickness suggests that some data may be obscured by assigning to a single fauna all collections that contain long-ranged *Homogalax*. It is fully recognized that the rate of sedimentation is not everywhere the same, especially during the deposition of continental sediments. Nevertheless, segregation of fossils from different levels of so thick a unit would be a useful practise in analyzing the faunas. Therefore, according to their stratigraphic position, these levels will be called lower, middle and upper Gray Bull simply on the basis of superposition (tables I, IV). But this subdivision of the Gray Bull, as well as the assignment of some material to particular levels, is quite arbitrary, hence the data should be used with utmost caution. Moreover, the stratigraphic ranges of some of the Gray Bull mammals are certain to be extended. Simpson (1937b, pp. 1–2) discovered that statistical methods reveal a slightly less advanced character of the "Sand Coulee" (lower Gray Bull) mammals when compared with middle and upper Gray Bull species. His conclusion is fortified by the generic ranges shown in table I. In fact an analysis of the Early Eocene fauna discloses that the Lysite (long recognized as a convenient faunal unit) and upper Gray Bull have a greater percentage of genera in common than do the upper and lower Gray Bull faunas.

Additional collections may evidence more unity within the Gray Bull fauna than is now suspected; it is also possible that they will show the lower Gray Bull to be even more distinct. If the latter proves to be the case, a subdivision of the Gray Bull beds and fauna should be devised.

Lower Gray Bull fossils (here combining Granger's Sand Coulee and lower Gray Bull) are preserved within the lower 500 feet of the Willwood formation. Most of the specimens have been recovered from exposures in the Clark Fork drainage in the northern part of the Big Horn Basin, along the Clark Fork-Shoshone divide and near the head of Big Sand Coulee. Fossils have also been found south of the Clark Fork in the vicintiy of Pat O'Hara Creek, on the Paint Creek-Pat O'Hara Creek divide, at the northeastern base of Heart Mountain, and at the southern end of Polecat Bench. Farther south in the basin, along the eastern extent of the Willwood formation, lower Gray Bull mammal remains have been collected from badland patches east of McCulloch Peaks, south of the Greybull River (particularly in the vicinity of Basin), and about 10 miles southeast of Worland.

Fossils from middle Gray Bull beds have been found in the extensive badlands around McCulloch Peaks and in the middle part of the drainages in the wasteland between Worland and the Greybull River.

Upper Gray Bull fossils are preserved in

beds on the upper slopes of McCulloch Peaks, at the northern base of Tatman Mountain, south of the Greybull River at the heads of the creeks flowing eastward from Tatman Mountain (especially Dorsey, Elk, Five Mile, and Ten Mile creeks), and in the lower levels of Buffalo Basin (upper Dry Cottonwood Creek drainage).

Members of six families of mammals first appeared in the Gray Bull fauna, at the beginning of Early Eocene time—the Erinaceidae, Adapidae, Hyaenodontidae, Equidae, Isectolophidae, and Dichobunidae. In addition, the family Arctostylopidae, known in North America only from lower Gray Bull beds, is represented by a single specimen.

Paleocene genera not known above the Gray Bull fauna are as follows: In lower Gray Bull only, *Prochetodon*, *Neoliotomus*, *Plesiadapis*, *Carpolestes*, *Phenacodaptes*, and *Probathyopsis*. In lower and middle Gray Bull, *Ectypodus*, *Dissacus*, and *Haplomylus*. Throughout the Gray Bull, *Thryptacodon* (see note 40), *Apheliscus* (?Almagre also).

Gray Bull genera in older and younger faunas are *Diacodon*, *Palaeosinopa*, *Esthonyx*, *Phenacolemur*, *Palaeanodon*, *Paramys*, *Oxyaena*, *Didymictis*, *Phenacodus*, *Ectocion*, and *Coryphodon*. *Meniscotherium* (see note 56) has not been recovered from Gray Bull beds, but it occurs in older and younger faunas.

Genera found only in the Gray Bull are as follows: In lower Gray Bull only, *Creotarsus*, a new genus in the Apatemyidae, *Dipsalidictides*, and *Arctostylops*. In lower and middle Gray Bull only, *Plagiomene* and *Palaeonictis*. In middle (or possibly lower) Gray Bull only, *Teilhardella*. Throughout the Gray Bull, *Homogalax*, *Pachyaena* (?Almagre also).

The following genera which begin in the Gray Bull continue into younger faunas: *Peratherium*, *Didelphodus*, *Nyctitherium*, *Entomolestes*, *Cynodontomys*, *Pelycodus*, *Tetonius*, *Paratetonius*, *Loveina?* (see note 23), *Ectoganus*, *Anacodon*, *Hapalodectes*, *Prolimnocyon*, *Sinopa*, *Miacis*, *Vulpavus*, *Uintacyon*, *Viverravus*, *Vassacyon*, *Hyopsodus*, *Hyracotherium*, *Diacodexis*, *Bunophorus*, and *Wasatchia*.

Species and subspecies found only in Gray Bull beds are as follows:

Ectypodus simpsoni
Ectypodus tardus
Neoliotomus conventus
Neoliotomus ultimus
Peratherium comstocki
Diacodon tauri-cinerei
Didelphodus absarokae absarokae (P[1]Almagre)
Didelphodus absarokae secundus (?Lysite also)
Creotarsus lepidus
Nyctitherium celatum (?Almagre, ?Largo also)
Palaeosinopa lutreola
Palaeosinopa veterrima
Apheliscus insidiosus (?Almagre, ?Largo also)
Plagiomene multicuspis
Pelycodus ralstoni
Pelycodus trigonodus
Phenacolemur citatus
Phenacolemur praecox
Teilhardella chardini
Loveina? vespertina (Almagre also)
Tetonius ambiguus
Tetonius homunculus
Paratetonius steini
Paratetonius tenuiculus
Ectoganus gliriformis (?Almagre, ?Largo also)
Palaeanodon ignavus (?Lysite also)
Paramys atwateri (PLost Cabin also)
Thryptacodon olseni
Dipsalidictides amplus
Palaeonictis occidentalis
Oxyaena transiens
Oxyaena gulo (Indian Meadows also)
Oxyaena intermedia
Dissacus navajovius longaevus
Pachyaena gigantea gigantea
Pachyaena gigantea ponderosa
Pachyaena gracilis
Pachyaena ossifraga (?Almagre, ?Largo also)
Hapalodectes leptognathus
Prolimnocyon robustus
Prolimnocyon atavus (P?Almagre, ?Lysite also)
Sinopa mordax
Sinopa opisthotoma
Sinopa shoshoniensis
Didymictis protenus leptomylus (?Gray Bull)
Didymictis protenus curtidens
Miacis exiguus
Viverravus politus

[1] P indicates provisional reference to the species.

Vassacyon promicrodon (PLost Cabin also)
Uintacyon massetericus rudis
Ectocion osbornianus osbornianus
Hyopsodus simplex (Indian Meadows also)
Hyopsodus miticulus (Almagre also)
Phenacodus robustus
Phenacodus primaevus intermedius (PAlmagre, PLost Cabin also)
Coryphodon cinctus
Coryphodon curvicristis
Coryphodon marginatus
Coryphodon cuspidatus (Almagre also)
Coryphodon latidens (Almagre, PLargo also)
Coryphodon testis (Almagre also)
Coryphodon sp. nov.
Probathyopsis successor
Arctostyops steini
Hyracotherium etsagicum (Indian Meadows also)
Hyracotherium montanum
Hyracotherium resartum
Homogalax primaevus
Homogalax protapirinus
Homogalax semihians
Wasatchia grangeri
Diacodexis laticuneus
Diacodexis robustus (?Lysite also)
Diacodexis nuptus (?Gray Bull)

Lysite Fauna

Granger, 1910, pp. 245–246.
Sinclair and Granger, 1911, pp. 103–105, 108.
Sinclair, 1912, pp. 60–63.
Granger, 1914, pp. 201–203.

Two mammalian faunas are preserved in the Wind River formation in the Wind River Basin, Wyoming. The older Lysite (table IV), of middle Wasatchian age, is characterized by the presence of the tapiroid ungulate *Heptodon*, and the absence of *Homogalax* and *Lambdotherium*. The Lysite beds in the vicinity of Bridger, Cottonwood, and Lysite creeks (north of the town of Lost Cabin) consist of 350 feet of red-banded strata. A few nondiagnostic fossils from Circle Draw, on the North Fork of the Wind River, in the northwestern part of the basin, may pertain to the Lysite fauna.

An assemblage similar to the Lysite fauna has been secured from the upper part of the Willwood formation in the Big Horn Basin. It contains about two-thirds as many species as the Wind River Lysite. Granger (1914, p. 202) estimated the Big Horn Lysite beds to be 400 to 500 feet thick in the central part of the basin where they outcrop on all sides of Tatman Mountain and in the great badlands to the south (Buffalo Basin) and extend east probably as far as Five Mile Divide. Lysite beds may also be present at the top of the high Y.U. Bench north of the Greybull River. Remains of *Heptodon* in the upper 200 feet of Willwood strata on McCulloch Peaks indicate that these beds are either Lysite or Lost Cabin.

No Lysite fossils have yet been discovered in the Jim Creek section of the Willwood on the North Fork of the Shoshone River, though they may be preserved in the 150 feet of beds separating the Gray Bull and the Lost Cabin strata. Indeed, current information discloses that the Lysite assemblage is the least distinctive Wasatchian fauna; its presence is determined in large part by negative evidence, the absence of *Homogalax* and *Lambdotherium*. Correlation of any strata with the Lysite beds must be made cautiously, for the certain presence of a Lysite equivalent is very difficult to establish.

There are no known genera restricted to the Lysite fauna. The earliest appearance of *Absarokius* and *Heptodon*, both of which continue into the Lost Cabin, distinguishes the Lysite from the Gray Bull fauna. The following diagnostic Wasatchian genera have not been discovered above the Lysite: *Pelycodus* (Largo also), *Paratetonius*, *Ectoganus* (Largo also), *Anacodon*, and *Wasatchia* (Largo also). The genera present in both Gray Bull and Lost Cabin or Bridger faunas but not definitely known from the Lysite are: *Peratherium*, *Didelphodus* (?Lysite), *Nyctitherium*, *Palaeosinopa*, *Tetonius*, *Loveina*, *Palaeanodon* (?Lysite), *Vassacyon*, *Prolimnocyon* (?Lysite), *Miacis*, and *Ectocion*.

The following species and subspecies have been found only in Lysite beds:
Omomys? minutus (see note 24)
Paratetonius musculus (PGray Bull also)
Absarokius abbotti
Anacodon cultridens
Didymictis altidens lysitensis
Paramys excavatus (PGray Bull, PLost Cabin also)
Sciuravus depressus (see note 38)

Hyopsodus wortmani minor
Hyopsodus powellianus browni (PLost Cabin also)
Heptodon posticus (?Lost Cabin also)
Wasatchia lysitensis

Lost Cabin Fauna

Granger, 1910, pp. 241–245.
Sinclair and Granger, 1911, pp. 103–105, 108–109.
Sinclair and Granger, 1912, pp. 60–62.
Granger, 1914, p. 202.

The earliest collections of fossil mammals from the Wind River Basin were all from the upper part of the Wind River formation. This Lost Cabin fauna (late Wasatchian) is distinct from the Lysite assemblage, which occurs in lower strata. It is identified by the presence of *Lambdotherium*, the most primitive titanothere (see table IV). The Lost Cabin fauna has been recorded from 400 feet of variegated beds in the vicinity of Alkali Creek 5 miles north of Arminto in northwestern Natrona County, and north of Moneta in northeastern Fremont County, Wyoming. Lost Cabin mammals have also been found along Muddy Creek 10 miles north of Pavillion, and in the northwestern part of the Wind River Basin in Badland Gulch in sec. 12, T. 41 N., R. 106 W. (Love, 1939, p. 65). Along the southern margin of the basin there are about 250 feet of Lost Cabin beds at the base of Beaver (or Sweetwater) Divide, southern Fremont County.

In the Big Horn Basin the upper 325 feet of the Willwood formation on Tatman Mountain and in the Squaw Buttes area yield a Lost Cabin assemblage. The uppermost 200 feet of Willwood strata on McCulloch Peaks are either Lysite or Lost Cabin beds. Only about one-third as many species have been secured from the Big Horn Lost Cabin as from the Wind River Lost Cabin.

Genera from older and younger faunas that are found in Lost Cabin beds or are inferred to have lived during late Wasatchian time are *Peratherium*, *Entomolestes*, *Nyctitherium*, *Paramys*, *Sinopa*, *Miacis*, *Uintacyon*, *Viverravus*, *Vulpavus*, and *Hyopsodus*.

The following genera from older faunas have not been discovered above the Lost Cabin or equivalent faunas: *Diacodon Didelphodus*, *Palaeosinopa*, *Cynodontomys*, *Esthonyx*, *Phenacolemur*, *Tetonius*, *Absarokius*, *Loveina*, *Palaeanodon*, *Oxyaena*, *Ambloctonus*, *Hapalodectes*, *Prolimnocyon*, *Didymictis*, *Vassacyon*, *Phenacodus*, *Ectocion*, *Coryphodon*, *Meniscotherium*, *Hyracotherium*, *Heptodon*, *Bunophorus*, and *Diacodexis*.

The following genera occur only in late Wasatchian faunas: *Paricops*, *Shoshonius*, *Tubulodon*, *Protopsalis*, *Bathyopsis* (see note 63), and *Lambdotherium*.

Genera known first from the Lost Cabin that continue into younger (Bridgerian) faunas are: *Notharctus*, *Stylinodon*, *Tritemnodon*, *Eotitanops*, and *Hyrachyus*.

The following species and subspecies have been found only in the Lost Cabin beds:
Diacodon bicuspis (PGray Bull, P?Almagre also)
Didelphodus absarokae ventanus
Paricops multicuspis
Cynodontomys scottianus
Esthonyx acutidens
Notharctus venticolus
Notharctus nunienus
Loveina zephyri
Shoshonius cooperi
Tetonius barbeyi
Absarokius noctivagus
Stylinodon cylindrifer
Tubulodon taylori
Mysops kalicola (see note 39)
Oxyaena ultima
Ambloctonus major
Protopsalis tigrinus
Prolimnocyon antiquus
Tritemnodon whitiae
Didymictis altidens altidens (PKnight, PHuerfano A also)
Ectocion superstes (PGray Bull also)
Meniscotherium chamense chamense (Largo also)
Hyopsodus wortmani wortmani (PIndian Meadows also)
Hyopsodus walcottianus
Coryphodon singularis
Coryphodon ventanus (PHuerfano A also)
Coryphodon wortmani
Bathyopsis fissidens (see note 63)
Hyracotherium venticolum
Lambdotherium primaevum
Lambdotherium popoagicum (Huerfano A, La Barge also)
Lambdotherium priscum (Huerfano A also)
Lambdotherium progressum (Huerfano A also)
Lambdotherium magnum (Huerfano A also)
Eotitanops borealis

Eotitanops major
Eotitanops princeps
Eotitanops brownianus (Huerfano A or B also)
Eotitanops gregoryi
Heptodon calciculus
Heptodon brownorum
Diacodexis secans
Diacodexis olseni

Additional Wasatchian Faunas

Powder River Basin local faunas.—Early Eocene deposits in the Powder River Basin, Wyoming, have yielded *Pelycodus*, *Ectocion*, *Coryphodon*, and *Hyracotherium* in the vicinity of Sussex, Johnson County, and *Diacodexis* from strata interbedded with the Kingsbury conglomerate, about 600 feet above the base, near Sheridan, Sheridan County. *Coryphodon* was recovered from the variegated sediments, 2400 feet thick, at Pumpkin Buttes in Campbell County. (See Wood *et al.*, 1941, p. 49; Jepsen, 1940, p. 241–242.)

Until some diagnostic Wasatchian fossils are obtained from these localities the collections cannot be correlated precisely with other Early Eocene faunas.

Big Horn Basin local faunas.—Three molar teeth referable to the genus *Heptodon* establish the presence of either Lysite or Lost Cabin beds at the top of McCulloch Peaks. Although the specimens were found at least 2000 feet above the base of the Gray Bull beds, they are the only diagnostic post-Gray Bull fossils yet recovered from the McCulloch Peaks section. A third upper molar, U. S. National Museum no. 15847, was originally referred to *Helaletes*. "Re-examination leaves it as indeterminate between *Helaletes* and the most *Helaletes*-like species of *Heptodon*. Hence the McCulloch Peak local fauna is best interpreted as of Lost Cabin age" (Wood *et al.*, 1941, p. 25). Two upper molars of *Heptodon* (in the Princeton Museum collection) from the upper 200 feet of the high middle peak closely resemble some specimens of the genus in Lost Cabin collections. Nevertheless, in the absence of more diagnostic material, the McCulloch Peaks local fauna might be either Lysite or Lost Cabin.

Hyopsodus and the Wasatchian guide fossil *Hyracotherium* were found north of the Greybull River, near the center of sec. 18, T. 48 N., R. 103 W., in the belt of Willwood deposits along the eastern escarpment of the Absaroka plateau (Pierce and Andrews, 1941, p. 137). Undoubtedly these red-banded strata beneath the volcanic series were once continuous with the Willwood formation in the central part of the Big Horn Basin (Van Houten, 1944, p. 199–200).

Local faunas from the North Fork region.—The North Fork and the South Fork of the Shoshone River have cut deep recesses in the eastern edge of the Absaroka volcanic plateau where Willwood deposits now crop out beneath the Early Acid Breccia and the Early Basic Breccia.

The Jim Creek section of the Willwood formation (1000–1200 feet thick) on the north side of the North Fork of the Shoshone River, 18 miles west of Cody, Park County, Wyoming, yields Gray Bull and Lost Cabin fossils (Jepsen, 1939, p. 1914; Pierce, 1941, p. 2039–2041; Van Houten, 1944, p. 204).

Homogalax, diagnostic of the Gray Bull fauna, was found in a massive sandstone layer 250 feet above the base of the formation.

About 400 feet above the base (150 feet higher than the known Gray Bull beds) the Lost Cabin fossils *Lambdotherium* cf. *L. popoagicum*, *Hyracotherium*, *Coryphodon*, and *Paramys* were found in variegated shale. Seventy five feet higher in the Lost Cabin beds *Hyracotherium* (young individual), *Cynodontomys*, *Paramys*, a hyopsodontine condylarth, an omomyine primate, and a lizard were secured from a "quarry" in a drab layer.

No Lysite fauna has been discovered in the Jim Creek section, although it may be preserved in the 150 feet of strata separating the known Gray Bull and Lost Cabin beds.

Local faunas from the South Fork region.—Outliers of the Early Acid Breccia in the South Fork region, 30 miles southwest of Cody, have yielded fragmentary mammal remains (Jepsen, 1939; Van Houten, 1944, p. 202–203). Here the acid breccia rests conformably on the Willwood and is overlain by the Early Basic Breccia. From exposures of a tuffaceous facies along Aldrich Creek and at the eastern end of Ishawooa Mesa on Ishawooa Creek, the following fossils were collected: *Hyopsodus* cf. *H.*

paulus, fragmentary titanothere teeth, a stout *Paramys* incisor and molar larger than any known Early Eocene rodent teeth, and a scrap of a stylinodontid type of incisor. The material suggests a late Wasatchian or early Bridgerian age. Dorf (1939, p. 1907) believes the Early Acid Breccia flora is Early Eocene.

A few mammal teeth were found at the base of the Early Basic Breccia on Ishawooa Mesa (Van Houten, 1944, p. 203–204). The collection includes a small rodent incisor, a molar of *Microsyops* (a Bridgerian genus), and a molar of *Didymictis*, a Torrejon to Lost Cabin genus whose species become progressively larger during the Early Eocene. This *Didymictis* tooth is larger than any found in the Lost Cabin. Nevertheless, until the Bridgerian occurrence of the genus is established on more substantial evidence *Didymictis* is probably best considered as not ranging into the Middle Eocene. These specimens from the Early Basic Breccia suggest a Lost Cabin or Bridger age; plant remains from the basic breccia (Dorf, 1939) indicate a Middle Eocene (Bridgerian) age.

Local fauna from Wind River Basin.—The variegated Indian Meadows formation (Denison, 1937; Love, 1939, pp. 58–63) outcrops north of Dubois in the northwestern part of the Wind River Basin. Mammals found near the middle of T. 6 N., R. 6 W., in strongly tilted Indian Meadows strata overlain by the nearly horizontal Wind River formation, and 1½ miles above the mouth of Dinwoodie Creek in the SW¼ T. 6 N., R. 5 W., indicate that the deposits are equivalent to the lower Gray Bull beds.

The assemblage so far includes (table IV):
Esthonyx bisulcatus
Oxyaena gulo
cf. *Pachyaena*
Phenacodus sp.
Haplomylus speirianus
Hyopsodus simplex
Hyopsodus latidens
Hyopsodus cf. *H. wortmani*
Coryphodon cf. *C. elephantopus*
Hyracotherium etsagicum
Diacodexis chacensis

Bridger Basin local faunas.—Late Wasatchian mammal remains occur in variegated Knight deposits, 500 feet thick, in southernmost Sublette County, Wyoming, north of La Barge on the Green River (Bonillas, 1936, p. 139). The area was mapped as Knight formation by Schultz (1914, pl. 1) after a small southwestern portion had been so mapped by Veatch (1907, pl. 3). Presumably, then, La Barge beds are part of the Knight formation, although they are 75 miles from the type locality.

The following forms constitute the La Barge local fauna: *Hyopsodus, Meniscotherium, Coryphodon, Hyracotherium, Heptodon, Lambdotherium popoagicum*, a tarsiid primate, and a taeniodont.

Fragmentary Wasatchian fossils have been collected from the Knight formation (1500 feet thick) in its type area in southwestern Uinta County, Wyoming. Most of the following specimens were found 6 miles east of Evanston and 6 miles north of Knight, Wyoming, about 500 feet above the base of the formation:
Diacodon sp.
Cynodontomys sp.
Didymictis cf. *D. altidens*
Hyopsodus sp.
Phenacodus primaevus primaevus
Coryphodon elephantopus
Coryphodon hamatus
Coryphodon radians
Coryphodon semicinctus
Meniscotherium robustum
Hyracotherium vasacciense
Heptodon sp.
Diacodexis sp.

Granger (1914, p. 203) correlated these fossiliferous beds with the Lysite on the basis of the presence of *Heptodon* and the absence of *Lambdotherium*. But the small collection is not diagnostic; it might be either a middle or a late Wasatchian fauna. Recovery of the fossils from the lower 500 feet of the type Knight formation seems to corroborate the suggested correlation with earlier Wasatchian assemblages, and also suggests that a late Wasatchian fauna may be preserved in the upper 1000 feet of variegated strata in the type area. Nevertheless, correlation based only on stratigraphic succession is unreliable when not substantiated by paleontologic evidence. In view of the established late Wasatchian age of the La Barge local fauna and the similarity of the La Barge and the type Knight assemblages,

the fossiliferous Knight strata east of Evanston are tentatively considered equivalent to Lost Cabin rather than Lysite beds. Both middle and late Wasatchian faunas may be preserved in the Knight formation, but the known fossils (table IV) do not indicate the presence of two distinct faunas.

Washakie Basin local faunas.—"Dad local fauna, Wasatchian, western Carbon County, Wyoming. Wasatchian mammals have been found east of the Washakie Basin, in the general neighborhood of Dad P.O., just under the Tipton tongue of the Green River" formation (Wood *et al.*, 1941, p. 18). The occurrence of the Dad local fauna in uppermost "Wasatch" strata suggests that the collection may correlate with some later Wasatchian fauna.

Coryphodon armatus, *Hyracotherium pernix*, *Parahyus aberrans* and *P. vagus* (see note 76) were recovered from "Wasatch" beds near Black Buttes and Bitter Creek on the northwestern rim of the Washakie Basin (Matthew, 1909, pp. 94–95). The red-banded "Wasatch" deposits here are 2000–3000 feet thick and interfinger at the top with the Green River formation. Marsh (1876, p. 402; 1894, p. 261) reported *Hyracotherium pernix* (an unrecognizable species) from "lowest Eocene of Wyoming" and the specimens of *Parahyus* from "lower Eocene of Wyoming," but in the absence of diagnostic fossils these local faunas cannot be correlated precisely with other Wasatchian collection.

Local fauna from Laramie Basin.—"Cooper Creek local fauna, Wasatchian; Albany County, Wyoming" (Wood *et al.*, 1941, p. 18). Variegated beds in Cooper Lake basin in the northern part of the Laramie Basin yield fossils characteristic of the Lysite or Lost Cabin (Nace, 1936, pp. 54–55).

Uinta Basin local faunas.—*Hyracotherium* and *Coryphodon* were found in a long spur of the "Wasatch" that lies on the eastern margin of the Uinta Basin, west of the Rangely anticline, in northwestern Rio Blanco County, northwestern Colorado (Dr. John Clark, personal communication). These "Wasatch" beds are Early Eocene and probably older than late Wasatchian, because the overlying Green River strata yield a late Wasatchian assemblage.

Green River lacustrine sediments above the "Wasatch" on the eastern rim of the Uinta Basin have yielded mammalian fossils (Burke, 1938, p. 14). *Lambdotherium* sp. and *Tetonius* (?) sp. were recovered from sandstone in the Douglass Creek member of the Green River, about 100 feet above variegated "Wasatch" deposits, in sec. 5, T. 7 S., R. 25 E., S.L.M. (one mile east of Powder Springs in SW¼SW¼ sec. 31, T. 6 S., R. 25 E., S.L.M.), 15 miles southeast of Jensen, Uintah County, eastern Utah. This evidence reveals that the lower part of the Green River formation in this region probably correlates with the Lost Cabin beds in Wyoming, thus demonstrating the existence of the Green River lake in the Uinta Basin in late Wasatchian time. Present data show that lake deposition began earlier here than in the Piceance Creek basin to the east, for there red-banded fluviatile deposits yield a late Wasatchian fauna.

In sec. 8, T. 7 S., R. 25 E., S.L.M., 2 miles southeast of Powder Springs, a Bridgerian local fauna comprising *Nyctitherium*, *Notharctus matthewi*, *Paramys*, *Sciuravus?* n.sp., and *Hyopsodus minusculus* was discovered in the Evacuation Creek member of the Green River, 1000 feet above the base of the formation.

Piceance Creek Basin local faunas.—The following Early Eocene species were recovered from the DeBeque formation (to be named and described by Patterson) in the Piceance Creek Basin near Rifle, Garfield County, Colorado, west of the Grand Hogback (J. LeRoy Kay, personal communication):

Didelphodus absarokae
Pelycodus tutus
Ectoganus simplex
Paramys excavatus
Oxyaena forcipata
Coryphodon anax
Coryphodon radians
Phenacodus primaevus
Meniscotherium tapiacitis
Hyopsodus sp.
Hyracotherium boreale
Hyracotherium montanum
Hyracotherium etsagicum
Hyracotherium craspedotum
Homogalax primaevus

Patterson (personal communication) dis-

covered at least two distinct faunal levels in the Wasatchian part of the DeBeque formation. The upper fauna includes the late Wasatchian *Parictops*, *Notharctus*, and titanotheres; *Meniscotherium* is sparingly represented. In the lower level *Meniscotherium* is relatively abundant.

A few nondiagnostic fossils were found in beds between the lower faunal level and the Paleocene (Plateau Valley beds) part of the formation. *Homogalax* in the Carnegie Museum collection suggests that these intervening beds may be equivalent to the Gray Bull (assuming that this perissodactyl has the restricted stratigraphic range here that it has in Wyoming).

The upper fauna from the DeBeque formation is undoubtedly of late Wasatchian age. The lower fauna, from beds above a possible Gray Bull correlative, may be middle Wasatchian. Abundant *Meniscotherium* in the lower fauna from the DeBeque and in the Largo (upper) fauna from the San Juan Basin, suggests that these two assemblages are about the same age, although the abundance of *Meniscotherium* in each collection may relate to favorable conditions of preservation at different times or to similar facies of different ages. The known fossil record of *Meniscotherium* is so erratic that the presence of the genus cannot be used as a reliable basis of correlation. *Meniscotherium* is sparsely represented in the late Wasatchian faunas from the Wind River (Lost Cabin) and Piceance Creek (upper level) basins. It is absent from the Middle Wasatchian (Lysite) of the Wind River Basin and abundant in the ?Middle Wasatchian (lower level) of the Piceance Creek Basin. In the San Juan Basin *Meniscotherium* is abundant in the upper level (Largo) and absent from the lower (Almagre). The species from the Bridger Basin is from either a Lysite or Lost Cabin equivalent. Moreover, the genus is probably present in late Paleocene collections but has not been reported from the early Wasatchian (Gray Bull) assemblage.

Huerfano Basin local fauna.—The Huerfano formation in the Huerfano Basin, Huerfano County, south-central Colorado, consists of 3500 feet of red-banded sediments. In the upper 700–800 feet two faunal levels have been recognized. Beds that yield the Huerfano A fauna (Osborn, 1897, pp. 247–258; 1919, pp. 557–559) (table IV), equivalent to the Lost Cabin, are about 200 feet thick and outcrop 2 miles east and southeast of Gardner and in the Garcias Canyon region 1½ miles south of Talpa.

The identifiable Huerfano A mammals are:

Cynodontomys sp.
Esthonyx sp.
Notharctus sp.
Stylinodon sp.
Paramys cf. *P. copei*
Oxyaena forcipata
Oxyaena lupina
Hapalodectes sp.
Didymictis cf. *D. altidens*
Viverravus dawkinsianus
Phenacodus sp.
Hyopsodus cf. *H. powellianus*
Coryphodon cf. *C. ventanus*
Hyracotherium sp.
Lambdotherium popoagicum
Lambdotherium priscum
Lambdotherium progressum
Lambdotherium magnum
Heptodon sp.
Diacodexis sp.
Eotitanops brownianus (possibly from Huerfano B)

The Huerfano B fauna of Bridgerian (Middle Eocene) age was obtained from exposures of the uppermost 500 feet of the formation 2–3 miles west and northwest of Gardner. The following Wasatchian genera have been reported from the Huerfano B fauna: *Heptodon*, *Didymictis*, *Cynodontomys*, *Diacodexis*, *Hyracotherium*, *Bunophorus*, and *Wasatchia*. If the specimens are correctly identified and are not Huerfano A material mixed in collecting, their occurrence suggests either that mammals restricted elsewhere to the Early Eocene lingered into the Middle Eocene here, or that genera supposedly diagnostic of the Middle Eocene appeared in late Wasatchian time in the Huerfano Basin.

San Juan Basin faunas.—The Canyon Largo (replaces "Wasatch," Wood *et al.*, 1941, p. 16) formation in the San Juan Basin in northwestern New Mexico and southwestern Colorado yields Tiffanian and Wasatchian faunas (Granger, 1914, pp. 205–206). No younger assemblages have been

reported from this basin. The Early Eocene fossils were recovered in the vicinity of Gallina, Ojo San Jose, and La Jara, Rio Arribas County, New Mexico, where the formation is about 1000 feet thick. The Tiffany fauna has been found only in the northernmost part of the basin.

Fossils preserved in the lower 650 feet of the Canyon Largo formation were collected from the greater part of the Almagre watershed and at the head of Arroyo Blanco. The Almagre fauna is larger than the Largo fauna and contains such common Wasatchian forms as *Sinopa*, *Coryphodon*, *Phenacodus*, and *Hyopsodus*. *Chriacus gallinae* is the only species limited to the Almagre. As yet *Meniscotherium* has not been discovered in Almagre beds.

The Largo fauna was secured from the upper 350 feet of the Canyon Largo formation at the head of Largo Arroyo and in the area west and southwest of Ojo San Jose drained by the Puerco River tributaries. *Meniscotherium* is especially common in these beds. *Meniscotherium tapiacitis* and *M. chamense terraerubrae*, as well as *Ambloctonus sinosus* (?Largo) and *A. hyaenoides*, are diagnositc.

Most of the Wasatchian fossils from the San Juan Basin were obtained by Cope's parties before the presence of two faunas was suspected. Consequently specimens from the upper and lower levels were mixed in collecting so that it is impossible to determine to which fauna much of the material belongs. Among such fossils the following occur only in Wasatchian deposits in the San Juan Basin: *Cynodontomys angulatus*, *Sinopa secundaria* (PGray Bull also), *Hyracotherium angustidens*, *H. validum*, *H. cristonense* (PGray Bull also), and *Phenacodus astutus*.

Pelycodus tutus and *Didymictis protenus protenus* have been found in both Almagre and Largo beds, but not elsewhere.

Hyracotherium is the only perissodactyl present in the Almagre and Largo faunas, suggesting that these assemblages may represent a facies different from the Wasatchian faunas of Wyoming, though most other common Wasatchian genera are known in the San Juan collections. In the absence of the diagnostic Wasatchian perissodactyls, *Homogalax*, *Heptodon*, and *Lambdotherium*, correlation of the Almagre and Largo faunas with other Early Eocene assemblages is difficult.

Many Almagre genera and species have upper Gray Bull and Lysite affinities; especially indicative are *Oxyaena*, *Anacodon*, *Uintacyon*, and *Vulpavus*. Yet a primitive character of the San Juan faunas is revealed by the presence of *Pachyaena*, *Apheliscus*, and *Chriacus*, otherwise known only from Gray Bull or older collections.

The Largo fauna has characteristics of both Lysite and Lost Cabin assemblages. *Ambloctonus* and several Lost Cabin species in the Largo suggest a late Wasatchian age. On the other hand, *Pelycodus*, *Ectoganus*, and *Wasatchia* in the Largo and otherwise limited to the Gray Bull and Lysite faunas, suggest a middle Wasatchian age. It is important to note, however, that the specimen of *Pelycodus frugivorus* from the Largo agrees rather closely with *Notharctus nunienus* (Matthew, 1915c, p. 440), and that *Pelycodus tutus* has not been found in Wyoming. Abundant *Meniscotherium* remains from the Largo beds may indicate correlation with the lower faunal level (probably a Lysite equivalent) in the DeBeque formation, though the absence of the genus from the type Lysite and its presence in the Lost Cabin suggest, on the contrary, that the Largo may be closer to the Lost Cabin. In view of the situation in the Piceance Creek Basin, however, the latter alternative does not appear reasonable. If correlation of the Largo with the lower faunal level of the DeBeque formation is correct, it serves as further evidence that the Largo fauna is middle Wasatchian, and that the Almagre probably is closely related to the Gray Bull fauna.

A possible explanation for some of the differences between the San Juan faunas and the Early Eocene assemblages from Wyoming may be found in the more southerly position of the Almagre and Largo beds. In a study of the Lancian (late Cretaceous) floras Dorf (1942, p. 101) was able to show that the Lance flora (from eastern Wyoming) has a somewhat less subtropical aspect than the Laramie plant remains from north-central Colorado, due to latitudinal control of vegetational zones. Moreover, the Hell Creek flora from southeastern Montana is slightly more temperate than the Lance.

This attempt to determine the relationship between the San Juan faunas and the better-known assemblages from Wyoming reveals some of the difficulties involved in an effort to establish a correlation of early Cenozoic mammalian faunas.

STATISTICAL ANALYSIS OF CLARK FORK, GRAY BULL, LYSITE, AND LOST CABIN FAUNAS

A list of the Clark Fork, Gray Bull, Lysite, and Lost Cabin genera arranged according to geologic range (table I) reveals several significant relationships. If a genus is a member of both older and younger faunas, it is presumed to be present in an assemblage and is indicated by a dashed line in the table in order to present the maximum continuity between the faunas. The generic distributions thus inferred are incorporated in the numerical analysis. The New Mexican faunal level in which *Apheliscus* and *Pachyaena* were found was not recorded, but inasmuch as other specimens of these genera have not been found above the Gray Bull, the genera are assumed to range no higher than Almagre and are counted in the Gray Bull list. Largo genera are likewise counted in the Lysite.

Statistics derived from table I are presented in tabular form.

STATISTICS DERIVED FROM TABLE I

	Clark Fork	Gray Bull	Lysite	Lost Cabin
Genera from older fauna dying out in this fauna	1	12	5	24
Genera from older fauna continuing through into younger fauna	17	12	31	10
Genera beginning in this fauna continuing into younger fauna	7	24	3	5
Genera diagnostic of this fauna	0	9	0	6
Total	25	57	39	45

No wholesale extinction of archaic Paleocene mammals occurred at the end of the Paleocene epoch. Instead, many members of ancient orders had disappeared before Clarkforkian (latest Paleocene) time and 95 percent of the Clark Fork genera continued into the Early Eocene. Two-thirds of these were long-ranged Paleocene forms, about half of which continued after Early Eocene time. The other half have not been recovered above the middle Gray Bull. The remaining one-third of the Clark Fork genera began in this fauna, and most of them persisted after the Early Eocene. According to these data the Clark Fork was truly transitional between the characteristic Tiffanian Paleocene fauna and the Early Eocene assemblage. Nevertheless, it is assigned to the Paleocene because a great many new genera began in the succeeding Gray Bull fauna.

Sixty percent of the Gray Bull genera appeared for the first time. It is the introduction of members of many "modern" groups that most conveniently marks the beginning of Eocene time, which in the Rocky Mountain region began with the appearance of Perissodactyla, Artiodactyla, the Adapidae and the Hyaenodontidae. Of the 33 genera whose earliest appearance was in the Gray Bull 70 percent continued into younger faunas, demonstrating that the Gray Bull is correctly considered close to later Wasatchian faunas. Moreover, these data show clearly that the Paleocene-Eocene division marks the beginning and early development of the great expansion of mammals in the Cenozoic era.

The least distinctive Wasatchian assemblage, that from the Lysite beds, was transitional between the Gray Bull and Lost Cabin, having about as many genera in common with the oldest as with the youngest Wasatchian faunas. In contrast to the many new forms in the Gray Bull only three new genera appeared in the Lysite, and these continued into the Lost Cabin.

Seventy-five percent of the Lost Cabin genera have been found in older Wasatchian faunas, whereas only 40 percent of the Gray Bull mammals were derived from the Clark Fork. About 50 percent of the Gray Bull and 80 percent of the Lysite genera that occurred

TABLE I.—GEOLOGIC RANGE OF GENERA

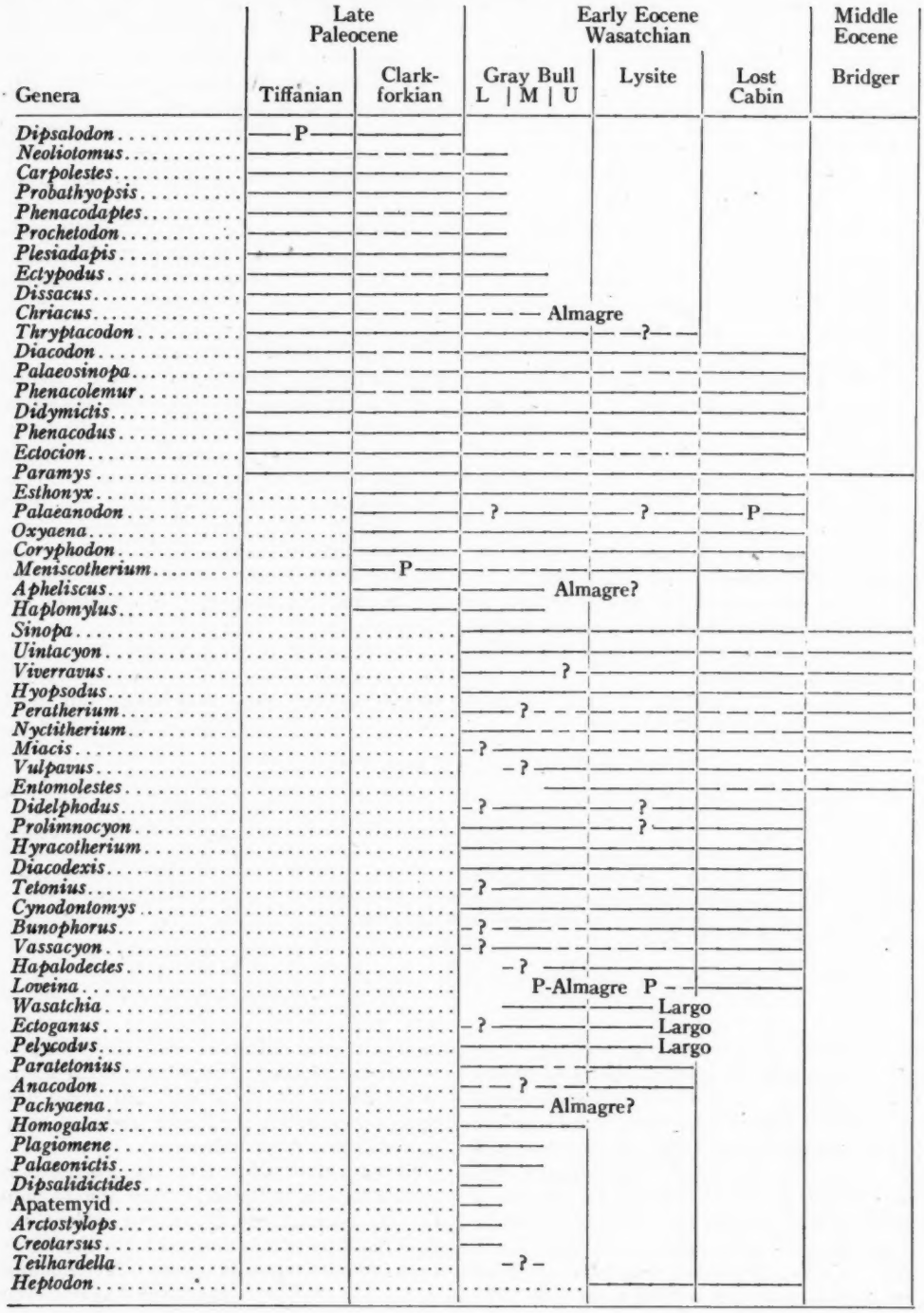


TABLE I.—*Continued*

Genera	Late Paleocene: Tiffanian	Late Paleocene: Clark-forkian	Early Eocene Wasatchian: Gray Bull L | M | U	Early Eocene Wasatchian: Lysite	Early Eocene Wasatchian: Lost Cabin	Middle Eocene: Bridger
Absarokius						
Ambloctonus				Largo		
Notharctus						
Stylinodon						
Tritemnodon						
Eotitanops						
Hyrachyus						
Parictops						
Shoshonius						
Tubulodon						
Protopsalis						
Bathyopsis						
Lambdotherium						
Parahyus			?	?	?	

P indicates provisional reference of a specimen to the genus.
? denotes uncertain faunal level.

in older faunas continued into younger faunas, yet only 25 percent of the Lost Cabin mammals found in older beds continued into the Middle Eocene. Furthermore, the Lost Cabin had the largest proportion of genera that did not continue into younger faunas—Gray Bull 38 percent, Lysite 12 percent, and Lost Cabin 66 percent.

DEFINITION OF PROVINCIAL AGE TERMS, CLARKFORKIAN AND WASATCHIAN

The definition of provincial age terms in "Nomenclature and correlation of the North American continental Tertiary" (Wood *et al.*, 1941) was an important advance in the study of Cenozoic stratigraphy. According to the latest information the definitions of Clarkforkian and Wasatchian ages are amended and amplified as follows:

Clarkforkian Age

Index fossil: *Dipsalodon matthewi.*

First appearance: *Apheliscus, Coryphodon, Esthonyx, Haplomylus,* (see note 56) *Meniscotherium, Oxyaena, Palaeanodon.*

Last appearance: *Dipsalodon.*

Characteristic fossils: *Didymictis, Ectocion, Esthonyx, Phenacodus, Plesiadapis, Probathyopsis, Thryptacodon.*

Wasatchian Age

Index fossils: *Absarokius, Ambloctonus, Anacodon, Bathyopsis, Bunophorus, Cynodontomys, Diacodexis, Didelphodus, Ectoganus, Hapalodectes, Heptodon, Homogalax, Hyracotherium, Lambdotherium, Pachyaena, Palaeonictis, Pelycodus, Plagiomene, Prolimnocyon, Tetonius, Vassacyon, Wasatchia.* Eleven rare genera known only from beds of Wasatchian age are not listed here (see table II).

First appearance: *Entomolestes, Eotitanops, Hyopsodus, Hyrachyus, Miacis, Notharctus, Nyctitherium, Peratherium, Sinopa, Stylinodon, Tritemnodon, Uintacyon, Viverravus, Vulpavus.*

Last appearance: *Apheliscus, Carpolestes, Chriacus, Coryphodon, Diacodon, Didymictis, Dissacus, Ectocion, Ectypodus, Esthonyx, Haplomylus, Meniscotherium, Neoliotomus, Oxyaena, Palaeanodon, Palaeosinopa, Phenacodaptes, Phenacodus, Phenacolemur, Prochetodon, Plesiadapis, Probathyopsis, Thryptacodon.*

RÉSUMÉ OF THE WASATCHIAN FAUNA

Members of all the orders of mammals, except those which probably originated in the Old World (Monotremata, Pholidota, Sirenia, Hyracoidea, Proboscidea, Cetacea, and Lagamorpha), are known to have lived in the Rocky Mountain region during Wasatchian time.

The fauna comprised four elements: In-

TABLE II.—CLARKFORKIAN, WASATCHIAN, AND BRIDGERIAN MAMMALIAN GENERA

	C	W	B
Multituberculata			
Ptilodontidae	(−)*	−	
Ectypodus	(×)	×	
Prochetodon	(×)	×	
Neoliotomus	(×)	×	
Marsupialia			
Didelphidae	(−)	−*	−*
Peratherium		×*	×*
Insectivora			
Deltatheridiidae	(−)	−	−
Didelphodus		×	
Phenacops			×
Erinaceidae		−	−
Entomolestes		×	×
Leptictidae	(−)*	−*	
Diacodon	(×)	×	
Parictops		×	
Nyctitheriidae	−	−*	−
Genus indet.	×		
Nyctitherium		×	×
Entomacodon			×
Myolestes			×
Centetodon			×
Centracodon			×
Pantolestidae	(−)	−*	−
Palaeosinopa	(×)	×*	
Pantolestes			×
Apheliscidae	−	−	
Apheliscus	×	×	
Mixodectidae	(−)	−	−
Cynodontomys		×	
Microsyops			×
Incertae sedis			
Creotarsus		×	
Tillodontia			
Tillotheriidae	−	−*	−
Esthonyx	×	×*	
Tillotherium			×
Trogosus			×
Anchippodus			?
Dermoptera			
Plagiomenidae	(−)	−	
Plagiomene		×	
Primates			
Adapidae		−*	−*
Pelycodus		×	
Notharctus		×	×
Aphanolemur			×
Prosinopa			×
Plesiadapidae	−*	−*	*
Plesiadapis	×*	×	
Incertae sedis			
Phenacolemur	(×)	×	
Trogolemur			×
Uintasorex			×
Apatemyidae	(−)	−*	−*
Teilhardella		×	
Genus nov.		×	
Apatemys			×
Carpolestidae	−	−	
Carpolestes	×	×	
Anaptomorphidae	(−)	−*	−*
Absarokius		×	
Loveina		×	
Paratetonius		×	
Shoshonius		×	
Tetonius		×	
Omomys			×
Anaptomorphus			×
Euryacodon			×
Hemiacodon			×
Uintanius			×
Washakius			×
Taeniodonta			
Stylinodontidae	(−)	−	−
Ectoganus		×	
Stylinodon		×	×
Edentata			
Metacheiromyidae	−	−	−
Palaeanodon	×	×	
Metacheiromys			×
?Tubulidentata			
Tubulodontidae		−	
Tubulodon		×	
Rodentia			
Ischyromyidae	−	−*	−
Paramys	×	×*	×
Reithroparamys			×
Pseudotomys			×
Sciuravus			×
Tillomys			×
Taxymys			×
Mysops			×
Pauromys			×
Carnivora			
Arctocyonidae	−*	−*	
Thryptacodon	×	×	
Chriacus	(×)	×	
Anacodon		×	
Oxyaenidae	−	−*	−
Dipsalodon	×		
Oxyaena	×	×	
Dipsalidictides		×	
Palaeonictis		×*	
Ambloctonus		×	
Protopsalis		×	
Patriofelis			×
Mesonychidae	−*	−*	−
Dissacus	×*	×*	
Pachyaena		×*	
Hapalodectes		×	
Mesonyx			×
Synoplotherium			×
Harpagolestes			×
Hyaenodontidae		−*	−*
Prolimnocyon		×	
Sinopa		×	×*
Tritemnodon		×	×
Limnocyon			×
Thinocyon			×
Machaeroides			×
Miacidae	−	−	−
Didymictis	×	×	
Vassacyon		×	
Miacis		×	×
Uintacyon		×	×
Viverravus		×	×
Vulpavus		×	×
Oödectes			×
Palaearctonyx			×

TABLE II.—*Continued*

	C	W	B
Condylarthra			
Phenacodontidae	–	–*	
Phenacodus	×	×*	
Ectocion	×	×	
Meniscotheriidae	–*	–	
Meniscotherium	×	×	
Hyopsodontidae	–	–	–
Phenacodaptes	(×)	×	
Haplomylus	×	×	
Hyopsodus		×	×
Pantodonta			
Coryphodontidae	–	–*	
Coryphodon	×	×*	
Dinocerata			
Uintatheriidae	–	–	–
Probathyopsis	×	×	
Bathyopsis		×	
Elachoceras			×
Uintatherium			×
Notoungulata			
Arctostylopidae		–	
Arctostylops		×	
Perissodactyla			
Equidae		–*	–
Hyracotherium		×*	
Orohippus			×
Brontotheriidae		–	–
Lambdotherium		×	
Eotitanops		×	×
Eometarhinus			×
Limnohyops			×
Manteoceras			×
Mesatirhinus			×
Palaeosyops			×
Telmatherium			×
Metarhinus			×
Isectolophidae		–	–
Homogalax		×	
Parisectolophus			×
Isectolophus			×
Helaletidae		–	–
Heptodon		×	
Helaletes			×
Dilophodon			×
Desmatotherium			×
Chasmotheroides			×
Hyrachyidae		–	–
Hyrachyus		×	×
Metahyrachyus			×
Colonoceras			×
Ephyrachyus			×
Hyracodontidae			–
Triplopus			×
Rhinocerotidae			?
Eotrigonias			?
Artiodactyla			
Dichobunidae		–*	–*
Bunophorus		×	
Diacodexis		×	
Wasatchia		×	
Homacodon			×
Sarcolemur			×
Microsus			×
Antiacodon			×
Stenacodon			×
?Ithygrammodon			×
Choeropotamidae		–	–
Parahyus		×	
Helohyus			×
Lophiohyus			×

( )—presence inferred.
* —also occurs in equivalent fauna of Europe.
Washakie B and Uinta A are considered to be Late Eocene (Uintan).

NUMERICAL RÉSUMÉ

	Clarkforkian	Wasatchian	Bridgerian
Orders	13	17	12
Families	26	38	28
Genera	26	72	82

	Families	Genera
From Clarkforkian into Bridgerian	16	1
From Clarkforkian into Wasatchian	10	23
Began Wasatchian	12	48
Wasatchian only	2	34
Continued into Bridgerian	10	14
Began Bridgerian	2	67

sectivores and didelphid marsupials were those persistently primitive forms of great antiquity that lived throughout Cenozoic time. A second element included more advanced Paleocene types which were common in the Early Eocene and persisted in abundance beyond that time. These were the early offshoots of the lemuroid and tarsioid primates, rodents, edentates, tillodonts and taeniodonts, uintatheres, hyopsodontids, and progressive creodonts. Of the 16 families ranging from Paleocene into Middle Eocene, most were of the latter category. There was only one such long-ranged genus, *Paramys* and this, perhaps, should be subdivided.

A third group of 10 families consisted of the multituberculates, primitive creodonts, aberrant insectivores and primates, pantodonts, and most of the condylarths, the diversified and rather specialized representatives of more ancient orders that lingered into the Early Eocene and then disappeared. These mammals composed a large part of the Wasatchian fauna.

The remainder of the fauna included hyaenodont creodonts, adapid primates,

perissodactyls and artiodactyls which first appeared in the Early Eocene. Nine families of these important later Cenozoic groups began in the Early Eocene and continued into the Middle Eocene, thus producing a significant change in the aspect of early Cenozoic faunas. (One family of insectivores is first known in the Early Eocene, and two families, the tubulodontids and arctostylopids, are each represented by a single specimen from Wasatchian deposits.)

During Wasatchian time archaic mammals were largely replaced by "modern" types, and in late Wasatchian some "modern" groups began to differentiate. The two new families and most of the 67 new genera that appeared in Middle Eocene resulted from this diversification.

A list of Clarkforkian, Wasatchian, and Bridgerian genera (table II) is presented to facilitate comparison of these successive North American faunas. Groups also represented in Late Paleocene, Early Eocene, or Middle Eocene faunas of Europe are so indicated by an asterisk. But it would not serve the purpose of this tabulation to include all known European or Mongolian families and genera of these ages. Some additional information regarding the Old World faunas is recorded in table III. The complete faunal lists are in Simpson's "Census of Paleocene mammals" (1936), "Paleocene and lower Eocene mammals of Europe" (1929), and "The principles of classification and a classification of mammals" (in manuscript, 1944).

DERIVATION OF THE EARLY EOCENE FAUNA

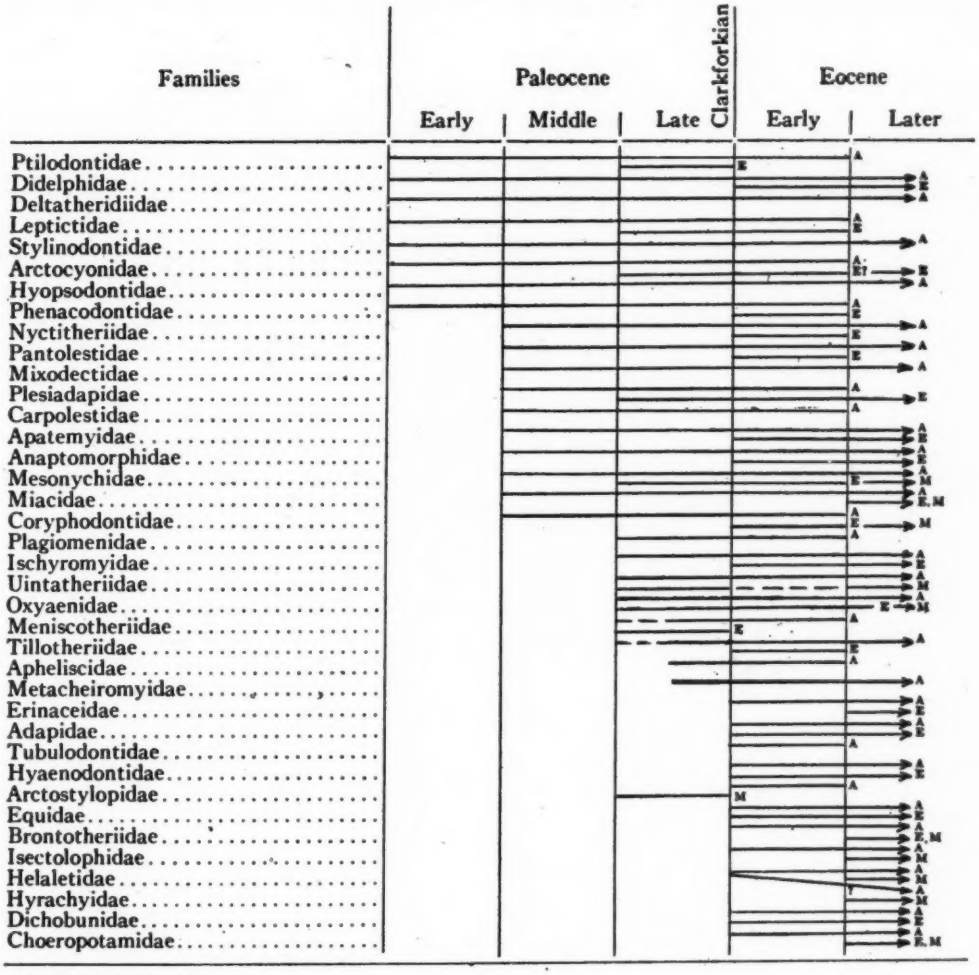
When North American Paleocene faunas were poorly known many "modern" mammalian families appeared for the first time in the Early Eocene record. As a consequence, these groups were thought to have been introduced by a great Early Eocene migration from an undiscovered center of evolution. But each new Paleocene collection vitiated this view. Indeed, Jepsen (1937, pp. 293–294) has cautioned that postulated invasions have often proved to be imaginary by the later discovery of ancestral forms in older rocks in the same area. He re-emphasized an alternative to migration to account for the appearance of new groups at a certain stratigraphic level, namely that the ancestors lived earlier in the same area but their remains have not been found. This absence may be laid to the fortunes of collecting or to differences of facies.

The rich assemblages from Middle and Late Paleocene strata revealed that some "modern" mammals were present in older North American faunas and did not migrate suddenly to this continent at the beginning of Early Eocene time. Discovery of the Clark Fork fossils necessitated still another modification of the presumed migration, for several Early Eocene genera in this latest Paleocene fauna had not been found in the older Tiffanian faunas. Accordingly, the invasion was interpreted to have begun in Clarkforkian time and to have been greatly reinforced in the Early Eocene. Comparison of the Clark Fork and Tiffanian collections proved to be misleading, however, because they were later found to represent dissimilar facies. The more recently discovered Plateau Valley mammals of Tiffanian age not only were members of the same facies as the Clark Fork mammals, but include large archaic subungulates which were supposedly immigrant Clarkforkian groups. Thus, the evidence fails to substantiate the postulated Clarkforkian invasion. In fact, a Plateau Valley coryphodontid proved to be a link between Middle Paleocene *Pantolambda* and *Coryphodon* (a genus once thought to be restricted to the Early Eocene because of its Early Eocene occurrence in Europe).

Current knowledge of the early Cenozoic ranges of families represented in the Early Eocene fauna is summarized in table III. Of the important groups once assumed to have migrated to North America at the beginning of the Eocene epoch, miacid creodonts, coryphodontids, and primates are now known in Middle Paleocene faunas; rodents, oxyaenid creodonts, uintatheres, and probably tillodonts in Late Paleocene Tiffanian faunas; and edentates in the Clark Fork fauna.

One of the greatest discontinuities in the Cenozoic record occurs between the Early and Middle Paleocene faunas (table III). Although the full significance of the apparently new Middle Paleocene families can not be determined because Early Paleocene collections are still too scanty, present evidence

TABLE III.—STRATIGRAPHIC RANGES OF FAMILIES REPRESENTED IN THE NORTH AMERICAN EARLY EOCENE FAUNA



A = North America
E = Europe
M = Mongolia

suggests that they were introduced by migration.

An Early Eocene invasion perhaps brought the adapid primates, hyaenodont creodonts, the perissodactyls and artiodactyls to North America, though even the artiodactyls may have been derived from an indigenous hyopsodont condylarth (Jepsen, 1937, p. 294). The synchronous appearance of the same genera and families in the Early Eocene of North America and Europe certainly testifies that a way of migration existed to permit free intermingling or immediate derivation from a common source. (See Simpson, 1929.) The similarity of these two faunas is emphasized by the marked difference between the Middle Eocene faunas of Europe and North America, suggesting submergence of the land connection that had linked the continents in Early Eocene time. Many Early Eocene families now represented in North American Paleocene as-

semblages are first known in Early Eocene collections in Europe (table III). Doubtless their apparent absence from European Paleocene collections is largely due to the meager Paleocene record of the Old World, though some of the groups may have been introduced from North America at the beginning of Early Eocene time.

Most of the known late Paleocene mammals of Mongolia were not directly ancentral to North American Early Eocene forms. Nevertheless, the presence of uintatheres and arctostylopids in Mongolia suggests that other North American groups may be discovered there. The failure to find ancestors of the Early Eocene immigrants in the poorly known Mongolian Paleocene does not necessarily eliminate Asia as an early Cenozoic center of dispersion. That a way of migration linked the continents at this time is suggested by the fact that in late Eocene time North American and Mongolian mammals migrated over a broad Alaskan land bridge that persisted through most of Cenzoic time.

INTERPRETATION OF EARLY EOCENE ENVIRONMENT

Faunal Facies

All the Clark Fork and almost all the Early Eocene mammalian fossils have been discovered by prospecting surface localities where

> the mammal remains are rare, as far as known, and are so sparsely scattered through the matrix that only accidental finds or concentration from long weathering and wind erosion leads to any production (Simpson, 1937a, p. 29).

In the Early Eocene collections from surface localities the most abundant forms are: *Coryphodon*, a hippopotamuslike "subungulate"; *Phenacodus*, a browsing archaic ungulate; *Hyracotherium*, the earliest horse; *Homogalax*, a tapiroid perissodactyl; *Lambdotherium*, the most primitive titanothere; the creodont carnivores *Oxyaena*, *Sinopa*, and *Didymictis; Hyposodus*, a small, clawed condylarth; and *Paramys*, a squirrellike rodent. Even though the larger terrestrial forms are well represented in these collections because they are more easily preserved, their relative abundance as fossils also indicates that they were conspicuous members of the Early Eocene fauna.

Several "pockets" or "quarries" have been discovered in carefully prospected Early Eocene deposits, yielding fragmentary jaws and skulls of small and minute animals that were mainly arboreal in habitus, though some were doubtless terrestrial forest dwellers. In each locality

> fossils are so concentrated in a local pocket that it is profitable to work the bed as a whole and recover fossils in place (Simpson, 1937a, p. 30).

The Early Eocene assemblages secured from three quarries in drab Gray Bull beds are remarkably uniform in composition. (See Van Houten, 1944, pp. 179–184.) *Ectypodus* (a specialized rodentlike multituberculate), possibly *Peratherium* (an opossumlike marsupial), the insectivore *Diacodon*, *Plagiomene* (a primitive dermopterid or an aberrant insectivore), and lizards are most frequently associated. *Nyctitherium* (a shrewlike insectivore), an apatemyid primate, *Pelycodus* (a primitive lemur), *Hyopsodus* and closely related *Haplomylus*, *Paramys*, *Diacodexis* (the oldest known artiodactyl), and *Hyracotherium* (young individual) have been found at quarry localities.

Another "quarry" fauna was recovered from a drab layer in the variegated Lost Cabin beds in the Jim Creek section of the Willwood formation, 18 miles west of Cody, Wyoming, containing the following mammals: *Hyracotherium* (young individual), *Paramys*, a small hyopsodontine condylarth, an omomyine primate, *Cynodontomys*, and lizards.

The absence of small specimens in collections from surface localities does not necessarily mean that small mammals did not live in the area or that they were not preserved along with the larger terrestrial mammals, for their remains may have been destroyed by weathering or overlooked in collecting. On the other hand, the absence of large mammals in the carefully prospected quarry localities indicates that there probably was no mingling of large and small mammals here.

Such a consistent difference in composition of Early Eocene surface and quarry collections suggests that two faunal facies are represented, though the quarry material is, as yet, too meager to permit determina-

tion of the real facies difference. But Simpson's interpretation of analogous Paleocene collections is pertinent. In his review of the Tiffany (Late Paleocene) fauna from southwestern Colorado, secured chiefly from a pocket in a drab layer in variegated beds, Simpson (1935, p. 5) noted the significant difference between quarry and surface material, showing that they represent dissimilar facies. His analysis showed clearly "that strata may be identical in age and yet have remarkably different faunas." Of the faunas from the Crazy Mountain field, Montana, the great majority of which comes from quarries, Simpson (1937a, pp. 62–63) states:

> This "surface fauna," 90 per cent carnivores and ungulates, is of more normal type, in comparison with Tertiary faunas generally, than are the quarry faunas. Its members average larger than do those of the quarry faunas, and they are probably terrestrial for the most part. This appears to be a normal flood-plain facies.

His analysis of the quarry material

> warrants the tentative conclusion that this fauna is largely aboreal, which is well in accord with the evidence that the quarries were in a swampy and heavily wooded area and would go far toward explaining the unusual facies of the quarry faunas.

Thus, it appears that two faunal facies are represented in Early Eocene collections. Members of an arboreal forest facies are concentrated in local pockets in drab layers, while large terrestrial mammals that lived in the savannahs are preserved as "surface" faunas sparsely scattered throughout the Early Eocene deposits. Recognition of these facies vitiates "absence of large forms" or "similarity of size" as criteria for determining the age of mammalian faunas.

Early Cenozoic Topography of the Rocky Mountain Region

The Laramide revolution was not a brief orogenic episode that produced an abrupt change in the topography of the Rocky Mountain region. Instead, intense deformation began in late Cretaceous time and continued into the early Cenozoic. But, although the basins were downwarped while many bordering structures were differentially elevated, deep erosion of the uplifts and concomitant aggradation of the basins to a high level relative to the ranges, produced a mature topography. As a consequence, warm-temperate to subtropical forests persisted in a humid, lowland environment during this period of diastrophism. To the east an embayment of the Gulf of Mexico extended northward up the Mississippi lowland in Paleocene and Early Eocene time.

During the Paleocene epoch luxuriant forests flourished in the intermontane basins, but in the Early Eocene open country inhabited by many ungulates and carnivores became more widespread in the lowlands. The same species of mammals lived in more than one basin, for no topographic barriers impeded the migration of the lowland animals. Most of the great thickness of waste-fill that accumulated in the basins was eroded from the surrounding mountains and deposited on flood plains and in river channels or in swampy woodland areas. Active volcanoes in the uplands spread tuff across western Wyoming. In Middle Eocene time extensive lakes and swamps, probably less than 1500 feet above sea level, filled the Big Horn, Bridger, Washakie, Uinta, and Piceance Creek basins. In some areas, in fact, the lacustrine sediments had begun to accumulate before the end of Early Eocene time. Deposition of sapropelic sediments in the lakes in Wyoming was terminated during the Middle Eocene by a tremendous outburst of volcanic ash and breccia in the Yellowstone Plateau area, recorded in the Bridger and Washakie formations and in the Early Basic Breccia of the Absaroka Range. But in northern Colorado and Utah great lakes apparently persisted during this period of volcanism.

Gradually, progressive regional uplift of the Rocky Mountain area (and the plains to the east) in later Cenozoic time, together with the accumulation of great volcanic deposits, provided a rain shadow that initiated the arid cycle now present. Slowly the lowland forests were displaced by grassy prairies, and, as deposition gave way to active erosion in the basins, coarse detritus was spread eastward across the Great Plains for the first time. As a consequence, Paleocene and Eocene deposits are largely confined to the intermontane basins, whereas later Cenozoic sediments are preserved on the plains.

Red-banded Deposits

One of the distinctive types of Early Cenozoic sediments in the Rocky Mountain intermontane basins is the red-banded fluviatile deposits. They consist of alternating red to buff and greenish or bluish-gray shale layers of variable thickness and extent, cut by numerous lenses of coarse yellow channel sandstone.

The red layers in the variegated early Cenozoic sediments have been interpreted to be the result of periodic aridity (see Sinclair and Granger, 1911, p. 113). This interpretation was based on the now discredited belief that red beds form only under arid conditions. But present evidence does not support this theory, for early Cenozoic floras, instead of indicating aridity, point to a humid, warm-temperate, lowland environment in the Rocky Mountain region.

A possible interpretation of the origin of red-banded deposits in a humid lowland, consistent with the paleontologic evidence, is suggested by the recurrence of large terrestrial mammals, mainly ungulates and creodonts, in variegated sediments, and of small arboreal forest animals in drab deposits and in gray layers in the variegated sediments. These observations strongly suggest that the gray layers accumulated in swampy woodlands, while the red layers were deposited on flood plains in savannahs that displaced the wooded areas from time to time.

According to this interpretation drab Paleocene sediments accumulated in swampy and heavily wooded lowlands, and in these swamp deposits small members of an arboreal forest facies are preserved. Lenses of coarse sandstone mark the channels of the aggrading streams. Locally, where flood plains were more extensive and lowland forests and grassland environments fluctuated, the variegated Puerco and Torrejon, Tiffany, Plateau Valley, and Clark Fork beds were deposited. From a "pocket" in drab Tiffany shale a forest faunal facies has been recovered. The other red-banded Paleocene deposits have yielded many ungulates and carnivores. In the Early Eocene widespread fluctuation of the forest and savannahs produced variegated sediments in most areas of accumulation. Again, arboreal forest animals were buried in drab swamp deposits and large terrestrial mammals in buff to red flood-plain sediments.

CONSPECTUS OF EARLY EOCENE MAMMALS

Three multituberculate genera lived in North America until after the beginning of Early Eocene time—the last representatives of this longest-lived order of mammals which had flourished throughout the Mesozoic and Paleocene in the Old and New Worlds. During their long history the small, rodentlike multituberculates possessed specialized, multicusped grinding teeth, yet retained extremely primitive skeletal structures.

Although opossumlike didelphid marsupials had become diversified in the Cretaceous period, their trituberculate molar pattern was almost stereotyped by Eocene time. Members of this group probably remained here to the present, but being mainly arboreal they left a scanty fossil record.

Early Eocene insectivores were common and of many different kinds. The leptictids, pantolestids, and mixodectids, as well as the very primitive deltatheridiids, were less diversified than in the Paleocene. The leptictids became extinct by the end of the Early Eocene and the other families continued to decline in the Middle Eocene. The shrewlike nyctitheriids, on the contrary, were rare in the Paleocene and Early Eocene and reached their peak in Middle Eocene time. *Entomolestes* (in Early and Middle Eocene time) was probably the first of the erinaceid insectivores—a group now living in Europe, Asia, and Africa. Late Paleocene and Early Eocene *Apheliscus* apparently belonged to still another line of insectivore evolution.

The plagiomenids, which first appeared in the Late Paleocene, possibly were ancestral to the modern Dermoptera. The only Early Eocene genus, *Plagiomene*, had specialized "dermopterid" incisors and multicusped molars. As yet, no later members of this family have been discovered.

Archaic tillodonts of Late Paleocene origin were represented in the Early Eocene of North America and Europe by a single genus, *Esthonyx*, an animal the size of a beaver. In Middle Eocene time tillodonts with low-crowned, insectivorelike cheek

teeth and a pair of scalpiform incisors, reached their maximum in size and number, and then disappeared.

The earliest primates were the diminutive Middle Paleocene plesiadapids, carpolestids, and apatemyids, offshoots, perhaps, of a lemuroid or protolemuroid stock, and the tarsioid anaptomorphids. The peculiar plesiadapids and carpolestids lived only until after the beginning of Early Eocene time. Anaptomorphid primates became abundant and diversified in the Early and Middle Eocene, but were rare in the Late Eocene. Possibly one member lived during Early Oligocene time. The specialized apatemyids never were abundant, though they, too, continued through the Eocene into the Oligocene. All these families, except the carpolestids, are known to have lived in Europe during early Cenozoic time.

At the beginning of Early Eocene time in Europe and North America there appeared the adapid primates with two incisors and an opposable thumb and great toe. These lemurs were common during Early and Middle Eocene and became rare in Late Eocene. *Pelycodus* probably was ancestral to *Notharctus*, one of the best-known fossil primates.

Several genera of the archaic taeniodonts lived in early Paleocene time; the last survivor continued into the Late Eocene. *Ectoganus* and *Stylinodon* in the Early Eocene had cylindrical, rootless cheek teeth and chisel-shaped incisors, not unlike a small ground sloth.

Late Paleocene and Early Eocene *Palaeanodon*, the earliest edentate, had simple, peglike cheek teeth. Doubtless, it was the ancestor of Middle Eocene *Metacheiromys* which resembled an armadillo.

Tubulodon was another insectivorous Early Eocene mammal. Certain features of its peglike teeth suggest that it may have been close to the ancestor of the tubulidentates, or may have represented a sterile branch from an archaic group ancestral to the condylarths and tubulidentates.

From an inconspicuous beginning in Late Paleocene time in North America the rodents became abundant, though but little diversified, in the Early Eocene of the Old and the New Worlds. When they first appeared the squirrellike ischyromyids, possibly ancestral to most later rodents, had the typical gnawing incisors. Several new genera began in the Middle Eocene but the principal modern groups did not appear until the Oligocene.

Creodont carnivores were common in Paleocene time, flourished in the Early Eocene, and reached their summit of development in Middle Eocene. Most of them had relatively large skulls but small brains, and many were ambulatory animals. Archaic arctocyonids had flattened, low-crowned crushing molars and sharp-pointed, uncleft ungual phalanges as in the insectivores. These primitive creodonts were abundant throughout much of Paleocene time and probably were ancestral to other creodont groups. Although North American members disappeared at the end of the Early Eocene, a possible Middle Eocene representative is known in Europe. Some genera, like *Chriacus* and *Thryptacodon* which continued into the Early Eocene, possessed lemurlike tritubercular teeth very similar to those of generalized primitive placentals, while *Anacodon*, with its piglike quadritubercular molars, had flanged lower jaws to protect elongate upper canines.

Long-faced, aberrant mesonychid creodonts appeared in the Middle Paleocene, characterized by high-cusped tritubercular (but nonshearing) molars. In Europe and North America primitive *Dissacus* in the Late Paleocene and Early Eocene and *Pachyaena* in the Early Eocene had plantigrade feet. But at the peak of mesonychid development in the Middle Eocene, members of this group were large-skulled, doglike runners with digitigrade feet and hooflike unguals cleft at the tip—the most specialized limbs among the creodonts. A Late Eocene Mongolian mesonychid was the largest of known Carnivora.

Large-brained, progressive and "adaptive" miacid creodonts, the first carnivores that possessed well-defined shearing teeth, began in the Middle Paleocene and became increasingly varied through the Eocene epoch in the Old and the New Worlds. All had a single pair of sectorial teeth (P^4 and M_1 as in true carnivores) and but slightly cleft unguals, and all were small, foxlike creatures. From the miacids true carnivores evolved. *Didymictis* and other

Paleocene genera were already too specialized to have been ancestral to the more generalized Early Eocene forms such as *Miacis* and *Uintacyon* that were close to the ancestral stock of the fissipeds (true carnivores).

Catlike oxyaenids appeared in Late Paleocene time, were common in the Early Eocene, reached great size and then disappeared in the Middle Eocene of North America but continued to the end of the epoch in Europe and Mongolia (here exceeded in size only by the contemporary Mongolian mesonychid). In this family of creodonts the face was short, the skull broad, and carnassial teeth were well developed, the body and tail were long, the limbs short. Blunt ungual phalanges bore deep clefts. There were two lines of descent which differed chiefly in the character of the teeth.

Hyaenodontid creodonts were already differentiated into two lines (broad-skulled and long-skulled) when they appeared in Europe and North America at the beginning of the Eocene epoch. The small, long-skulled, slender-bodied Early and Middle Eocene genera (e.g. *Sinopa* and *Tritemnodon*) had the characteristic sectorial teeth, plantigrade feet and sharp, cleft, clawed unguals. *Prolimnocyon* represented the broad-skulled line. Most later hyaenodontids were large and powerful (an Oligocene form from Canada is the largest-known American creodont); some were subdigitigrade runners, and some had flanged lower jaws suggesting a sabertooth modification of the upper canines. Despite the many true carnivores in later Cenozoic time the group was common in the Oligocene and one of these creodonts (a primitive type) survived into the Miocene epoch in India.

Primitive, small-brained condylarth ungulates first appeared in Early Paleocene and lingered into Late Eocene. The phenacodontids were most numerous in Late Paleocene time, just prior to the arrival of the earliest perissodactyls, and then died out in Early Eocene. That the phenacodontids included survivors of an ancient group that gave rise to "modern" ungulates is suggested by the structure of *Phenacodus* from the Late Paleocene and Early Eocene of North America and the Early Eocene of Europe. This was a cursorial mammal about the size of a small sheep, with crushing, piglike teeth, digitigrade feet, and small, flattened hoofs on each of its five toes. Other skeletal features were creodontlike. The smaller *Ectocion* of North America, also abundant in the Late Paleocene and less common in the Early Eocene, had cheek teeth similar to those of the oldest horse. *Meniscotherium* in the Late Paleocene and Early Eocene of North America, and related genera in the Late Paleocene of Europe, had specialized, crescentic grinding teeth, although the limbs were less advanced than in *Phenacodus*. Conservative hyopsodontids were those squirrellike condylarths that preserved the primitive clawlike unguals. They were common in Paleocene and Early Eocene time in North America. *Hyopsodus* continued in abundance into the Middle Eocene but died out by the end of the epoch.

Coryphodon, the only Early Eocene representative of the archaic pantodonts in North America and Europe, appeared in Late Paleocene time in North America. The largest mammal of its time, *Coryphodon* was nearly the size of an ox. It had a hippopotamuslike skull with an extraordinarily small brain case, large crested molars and heavy canine tusks, and five-toed, elephantine feet. Although *Coryphodon* was one of the most common Early Eocene mammals, it did not survive into the Middle Eocene. Related genera, however, are known from Late Eocene and Middle Oligocene deposits of Mongolia.

The oldest uintatheres lived in North America and Mongolia in Late Paleocene time. Members of this "subungulate" group increased in size during the Early Eocene, and after reaching their culmination in the Middle Eocene, when they were the largest, strangest-appearing, and among the commonest mammals, came to an end in Late Eocene as the titanotheres began their rise to prominence. Probably both *Probathyopsis* and *Bathyopsis* were five-toed and about the size of a tapir. They had peculiar ridged molars and long upper canine tusks protected by lower jaw flanges. On the skull were incipient bony protuberances.

A few specimens of *Palaeostylops* from the Late Paleocene of Mongolia, and a single jaw of *Arctostylops* from the earliest Eocene of North America, are the only record of the

notoungulates found outside of South America. The evidence suggests that these South American ungulates were derived from a group of mammals that evolved in Mongolia and migrated to North America and thence southward.

Perissodactyls appeared suddenly and in great abundance in Europe and North America at the beginning of the Eocene epoch. The typical long, slender face, quadritubercular molars, and fully unguligrade feet were already developed, and several lines of descent had diverged. All were much alike in form and proportion, none larger than the modern tapir; the principal difference was in the teeth. *Hyracotherium*, the "dawn horse," was especially abundant during Early Eocene time in the Old and New Worlds, while tapirlike *Homogalax* was restricted to North America. Later in Early Eocene time *Heptodon*, another tapiroid form, was common, hornless *Lambdotherium* and *Eotitanops* began the titanotheres (the most abundant Middle Eocene perissodactyls), and *Hyrachyus* was the first of the cursorial rhinoceroses. In Europe, too, several new families diverged during the Early Eocene; these lines were distinct from North American groups. Perissodactyls became even more numerous in Middle Eocene time, when they were the most abundant mammals in the fauna.

Artiodactyls also appeared for the first time in the Early Eocene. They may have been derived from a North American hyopsodont condylarth, or perhaps they migrated to Europe and North America along with the earliest horses and their allies. Among the dichobunid artiodactyls, only *Diacodexis* still had primitive tritubercular molars. *Parahyus* with its quinquitubercular cheek teeth probably was the first of the short-faced choeropotamids—close to the entelodonts. During Early Eocene time bunodont artiodactyls were not as abundant as perissodactyls. In the Middle Eocene they showed little evolutionary advance in North America, but in Europe, on the contrary, there were numerous and varied forms. In fact, the difference between North American and European Middle Eocene artiodactyls was so marked that there could have been no accessible migration route between the continents.

CLASSIFICATION AND DISTRIBUTION OF CLARKFORKIAN AND WASATCHIAN MAMMALS

In table IV all the species and subspecies of Clarkforkian and Wasatchian mammals are listed in a systematic classification arranged according to Simpson (1931a and MS), and supplemented by Osborn (1929), Simpson (1937a), Denison (1938), and Jepsen (1940). Because the data have been compiled from the literature and from museum catalogues, no attempt has been made to certify taxonomic identifications, except as noted. Generic and specific names followed by superior numbers are annotated in the notes on the faunal list at the end of table IV. P denotes that a specimen has been provisionally referred to a particular species, whereas cf. (compare) indicates the species which a specimen most closely resembles. A question mark has been inserted in the table when no exact information is available concerning the faunal level from which a specimen was obtained. Uncertainty arises most frequently with respect to material found in Almagre or Largo beds in the San Juan Basin, in Lysite or Lost Cabin beds of the Wind River Basin, and in Gray Bull, Lysite, or Lost Cabin beds in the Big Horn Basin. Most of these fossils were collected by Cope before the presence of more than one fauna was suspected. Under the Gray Bull fauna L, M, and U (lower, middle, and upper) indicate in which part of the 2000 feet of Gray Bull beds specimens of that species are known to have been preserved. The letters have been omitted in those instances where no precise information concerning the stratigraphic occurrence of the specimens within the Gray Bull has been recorded.

The following specimens have been omitted from the faunal list because none is considered adequate for establishing the presence of the genus or species; the material is either too poor for accurate identification or its locality is uncertain:

Clark Fork beds: *Bathyopsis*, *?Pelycodus*.

Gray Bull beds: cf. *Trogolemur*, *?Sarcolemur*, *?Mysops*, *Paramys delicatus?*, *P. delicatior*, *P. delicatissimus*, *Heptodon*, *Chriacus* (Hay, 1930, p. 461. Granger and Simpson, 1928, p. 1, call it *Pelycodus*), *Sarcolemur*

TABLE IV.—CLASSIFICATION AND DISTRIBUTION OF CLARKFORKIAN AND WASATCHIAN MAMMALS

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Multituberculata Cope, 1884											
Ptilodontidae Gregory & Simpson, 1926											
Ptilodontinae Jepsen, 1940											
Ectypodus[1] Matthew & Granger, 1921											
simpsoni	....	....	$\times^{M}_{L}$								
tardus	....	....	$\times_{L}$								
Prochetodon Jepsen, 1940											
cavus[2]	....	....	cf_{L}								
Gen. et sp. indet[3]	×										
Eucosmodontinae Jepsen, 1940											
Neoliotomus Jepsen, 1930											
conventus	....	....	$\times_{L}$								
ultimus	....	....	$\times_{L}$								
Gen. et sp. indet[4]	×										
Marsupialia Illiger, 1811											
Didelphidae Gray, 1821											
Didelphinae Simpson, 1927											
Peratherium[5] Aymard, 1850											
comstocki	....	....	$\times^{?}_{L}$								
Insectivora Bowdich, 1821											
Leptictidae Gill, 1872											
Diacodon Cope, 1875											
tauri-cinerei	....	....	$\times_{L}$								
alticuspis	....	....	....	?	....	×	....	?			
bicuspis	....	....	P^{U}	P?	....	....	....	....	....	×	
minutus[6]	....	....	cf_{L}								
sp.[7]	....	....	$\times_{L}$	....	....	....	×				
Parictops Granger, 1910											
mullicuspis	....	....	....	....	....	....	....	....	....	×	
Deltatheridiidae Gregory & Simpson, 1926											
Didelphodontinae Matthew, 1918											
Didelphodus Cope, 1882											
absarokae absarokae	....	....	$\times^{U\ M}_{M\ L}$	P							
absarokae secundus	....	....	$\times^{U}$	....	?						
absarokae ventanus	....	....	....	....	....	....	....	....	....	×	

[1] *Ectypodus*—genus revised by Jepsen, 1940, p. 258.

[2] *Prochetodon* cf. *P. cavus* (lower Gray Bull—Princeton Museum collection; see Jepsen, 1940, p. 327.

[3] Ptilodontinae gen. et sp. indet (Clark Fork)—Jepsen, 1940, p. 324.

[4] Eucosmodontinae gen. et sp. indet. (Clark Fork)—Jepsen, 1940, p. 324.

[5] *Peratherium*—assignment of lower jaws from Early Eocene deposits to this genus, rather than *Peradectes*, is tentative and based principally on the fact that the latter has not been reported above the Paleocene and the former is said to range from Early Eocene to Miocene. Enlargement of P2/2 relative to P3/3, characteristic of modern didelphids and incipient in *Peradectes*, is generally absent in *Peratherium* (Simpson, 1935, p. 12). Positive generic identification apparently depends on the nature of the upper molars. See Simpson, 1928, p. 3.

[6] *Diacodon*, cf. *D. minutus* (lower Gray Bull)—Princeton Museum collection.

[7] *Diacodon* sp. (lower Gray Bull; Knight formation)—Princeton Museum collection.

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Nyctitheriidae Simpson, 1928											
Nyctitherium Marsh, 1872											
celatum	....	....	$\times^{M}_{L}$	?	....	....	....	?			
Gen. et sp. indet[8]	×										
Pantolestidae Cope, 1884											
Pantolestinae Simpson, 1937											
Palaeosinopa Matthew, 1901											
lutreola	....	....	$\times^{U}_{M}$								
veterrima	....	....	$\times^{U}_{M}$								
didelphoides[9]	....	....	$\times^{M}_{L}$	×	....	....	....	....	....	×	
Apheliscidae Matthew, 1918											
Apheliscus Cope, 1875											
nitidus[10]	×	....	$\times_{L}$								
insidiosus	....	....	$\times_{U}$	?	....	....	....	?			
Mixodectidae Cope, 1883											
Cynodontomys Cope, 1882											
angustidens[11]	....	....	$\times^{U}_{L}$	....	....	....	....	....	....	?	
latidens[12]	....	....	P^{U}	....	×	×	....	....	....	×	
angulatus[13]	....	....	....	?	....	....	....	?			
scottianus	....	....	....	....	....	....	....	....	×	×	
sp.[14]	....	....	....	....	....	....	×	×	....	....	×
Erinaceidae Bonaparte, 1838											
Echinosoricinae Cabrera, 1925											
Entomolestes Matthew, 1909											
nitens	....	....	$\times^{U}$	....	....	×					
Incertae sedis											
Creotarsus Matthew, 1918											
lepidus	....	....	$\times_{L}$								
Tillodontia Marsh, 1875											
Tillotheriidae Marsh, 1875											
Esthonyx Cope, 1874											
latidens	×	....	$?_{L}$								
grangeri	×	....	$\times_{L}$								
bisulcatus[15]	P	×	$\times^{U}_{L}$	×	....	....	....	×			
acutidens	....	....	....	....	....	....	....	....	....	×	
sp.[16]	....	....	....	....	×	×	....	....	?	....	×

[8] Nyctitheriidae gen. et sp. indet. (Clark Fork)—Simpson, 1937b, p. 4.

[9] *Palaeosinopa didelphoides* (lower Gray Bull)—Princeton Museum collection. *Palaeosinopa didelphoides* (Almagre)—American Museum of Natural History collection.

[10] *Apheliscus nitidus* (lower Gray Bull)—Princeton Museum collection.

[11] *Cynodontomys angustidens* (?Lost Cabin, Wind River Basin)—Princeton Museum collection.

[12] *Cynodontomys latidens* (Lost Cabin, Wind River Basin)—Princeton Museum collection.

[13] *Cynodontomys angulatus*—type lost; "I have not recognized the genus with certainty from the New Mexican Wasatch" (Matthew, 1915c, p. 471). Cope's figure of *C.* (*Pelycodus*) *angulatus* does not seem to agree with *C. latidens*, although specimens referred to *C. angulatus* are *C. latidens* (p. 476).

[14] *Cynodontomys* sp. (Knight formation; Huerfano A)—American Museum of Natural History collection.

[15] *Esthonyx bisulcatus* (P Clark Fork; lower Gray Bull)—Some Clark Fork and lower Gray Bull specimens may be *E. spatularius* (if this Gray Bull species is valid) or may be an unnamed species (Simpson, 1937b, pp. 7–8).

[16] *Esthonyx* sp. (Lysite, Big Horn and Wind

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Dermoptera Illiger, 1811											
Plagiomenidae Matthew, 1918											
Plagiomene Matthew, 1918											
multicuspis	....	....	$\times^{M}_{L}$								
Primates Linnaeus, 1758											
Adapidae Trouessart, 1879											
Notharctinae Trouessart, 1879											
Pelycodus[17] Cope, 1875											
ralstoni	....	....	$\times_{L}$								
trigonodus	....	....	$\times^{M}_{L}$								
jarrovii	....	....	$\times^{M}_{L}$	×	×	×	....	??			
frugivorus	....	....	$\times^{U}$	×	×	×	....	×			
tutus[18]	....	....	....	×	....	....	....	×			
Notharctus[19] Leidy, 1870											
venticolus	....	....	....	....	....	....	....	....	....	×	
nunienus	....	....	....	....	....	....	....	....	×	×	
2 sp.	....	....	....	....	....	....	....	....	....	....	×
Plesiadapidae Trouessart, 1897											
Plesiadapis Gervais, 1877											
dubius	×										
cookei	×	....	$\times_{L}$								
fodinatus[20]	....	....	cf_{L}								
Apatemyidae Matthew, 1909											
Teilhardella Jepsen, 1934											
chardini	....	....	$\times^{?M}$								
Gen. et sp. nov.[21]	....	....	$\times_{L}$								
Carpolestidae Simpson, 1935											
Carpolestes Simpson, 1928											
dubius[22]	×	....	cf								
Anaptomorphidae Cope, 1883											
Omomyinae Wortman, 1904											
Loveina[23] Simpson, 1940											
zephyri	....	....	....	....	....	....	....	....	....	×	
? vespertina	....	....	$\times^{U}$	×							
Shoshonius Granger, 1910											
cooperi	....	....	....	....	....	....	....	....	....	×	
Omomys Leidy, 1869											
?minutus[24]	....	....	....	....	....	×					

River basins)—American Museum of Natural History collection.

Esthonyx sp. (?Lost Cabin, Big Horn Basin)—see note 49.

Esthonyx sp. (Huerfano A)—Osborn, 1919, p. 558.

[17] *Pelycodus*—not found above Lysite according to Matthew, 1915c, pp. 433–445, and Granger and Gregory, 1917, p. 844. Simpson, 1929, p. 9, records "*Pelycodus*, lower Gray Bull to Lost Cabin."

[18] *Pelycodus tutus*—Loomis, 1907b, p. 356, lists this species from the higher level (Gray Bull beds) of Tatman Mountain in the Big Horn Basin. Matthew, 1915c, p. 441, states, on the contrary, that *P. tutus* has not been found in Wyoming.

[19] *Notharctus*—not found below the Lost Cabin according to Matthew, 1915c, p. 442, and Granger and Gregory, 1917, pp. 844–845.

[20] *Plesiadapis* cf. *P. fodinatus* (lower Gray Bull)—Princeton Museum collection.

[21] Apatemyidae gen. et sp. nov. (lower Gray Bull)—Princeton Museum collection.

[22] *Carpolestes* cf. *C. dubius* (lower Gray Bull)—Princeton Museum collection.

[23] *Loveina*—Simpson, 1940, pp. 188–189.

[24] *Omomys? minutus* (Lysite, Wind River Basin)—It is unlikely that this species belongs in *Omomys* (Simpson, 1940, p. 189).

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Anaptomorphinae Wortman, 1904											
Tetonius[25] Matthew, 1915											
ambiguus	....	....	$\times^{?L}_{U}$								
homunculus	....	....	$\times^{U}_{M}$								
barbeyi	....	....	....	....	....	....	....	....	....	×	
Paratetonius[26] Seton, 1940											
steini	....	....	$\times^{?M}$								
musculus	....	....	P^{M}	....	....	×					
tenuiculus[27]	....	....	$\times_{L}$								
Absarokius Matthew, 1915											
abbotti	....	....	....	....	×	×	....	....			
noctivagus	....	....	....	....	....	....	....	....	×	×	
Incertae sedis											
Phenacolemur Matthew, 1915											
citatus	....	....	$\times^{U}_{M}$								
praecox	....	....	$\times^{M}_{L}$								
sp.[28]	....	....	....	....	....	×	....	....	....	×	
Taeniodonta Cope, 1876											
Stylinodontidae Marsh, 1875											
Stylinodontinae Schlosser, 1911											
Ectoganus Cope, 1874											
gliriformis	....	....	$\times^{?}_{M}$	?	....	....	....	?			
simplex[29]	....	....	×	?	×	....	....	?			
sp.[30]	....	....	....	×	....	....	....	×			
Stylinodon Marsh, 1874											
cylindrifer	....	....	....	....	....	....	....	....	....	×	
sp.[31]	....	....	....	....	....	....	....	....	P	....	×
Edentata Cuvier, 1798											
Metacheiromyidae Wortman, 1903											
Palaeanodon Matthew, 1918											
parvulus	×										
ignavus	....	....	$\times^{U}_{M}$	....	?						
?P. sp. indet.[32]	....	....	....	....	....	....	....	?	....	×	
?Tubulidentata Huxley, 1872											
Tubulodontidae Romer, 1933											
Tubulodon Jepsen, 1932											
taylori	....	....	....	....	....	....	....	....	....	×	

[25] *Tetonius*—genus revised by Seton, 1940, pp. 41–42.

[26] *Paratetonius*—Seton, 1940, pp. 39–41.

[27] *Paratetonius tenuiculus* (lower Gray Bull)—Species provisionally referred to this genus (Seton, 1940, p. 41).

[28] *Phenacolemur* sp. (Lysite, Wind River Basin)—Jepsen, 1934, p. 289.
Phenacolemur sp. (Lost Cabin, Wind River Basin)—Nace, 1936, p. 175.

[29] *Ectoganus simplex* (Lysite, Big Horn Basin)—Osborn, 1929, p. 70.

[30] *Ectoganus* sp. (Almagre, Largo)—American Museum of Natural History collection.

[31] *Stylinodon* sp. (P Lost Cabin, Big Horn Basin)—Sinclair and Granger, 1911, p. 108.
Stylinodon sp. (Huerfano A)—American Museum of Natural History collection.

[32] *?Palaeanodon* sp. indet. (?Largo; Lost Cabin, Wind River Basin)—Simpson, 1931, p. 301.

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Rodentia Bowdich, 1821											
Ischyromyidae Alston, 1876											
Paramys Leidy, 1871											
murinus[33]	....	....	×	....	....	....	....	....	....	?	
buccatus[34]	....	....	P	?	P	×	....	?	....	×	
excavatus	....	....	P	....	×	×	....	....	....	P	
copei[35]	....	....	×	×	....	×	....	....	....	×	cf
atwateri	....	....	×	....	....	....	....	....	....	P	
major major	....	....	×	....	×	×	....	×	....	×	
major quadratus[36]	....	....	....	....	?	×	....	....	×	×	
sp. indet.[37]	×										
Sciuravus Marsh, 1871											
depressus[38]	....	....	....	....	....	×					
Mysops Leidy, 1873											
kalicola[39]	....	....	....	....	....	....	....	....	....	×	
Carnivora Bowdich, 1821											
Arctocyonidae Murray, 1866											
Oxyclaeninae Matthew, 1937											
Thryptacodon Matthew, 1915											
antiquus[40]	×	....	×$^{U\,M}_{L}$	....	?						
olseni	....	....	×$^{U}_{M}$								
Chriacus Cope, 1883											
gallinae	....	....	....	×							
Arctocyoninae Giebel, 1855											
Anacodon Cope, 1882											
ursidens	....	....	×$^{U}_{?}$	P	×						
cultridens	....	....	....	....	×						
Oxyaenidae Cope, 1877											
Oxyaeninae Trouessart, 1885											
Dipsalidictides Denison, 1938											
amplus	....	....	×$_{L}$								
Oxyaena Cope, 1874											
platypa	×										
aequidens	×										
transiens	....	....	×$_{L}$								
gulo	....	×	×$^{M}_{L}$								
intermedia	....	....	×$^{L}_{M}$								
forcipata	....	....	×^{U}	×	×	....	....	?	×	....	×
lupina	....	....	....	×	....	P	....	×	....	....	×
ultima	....	....	....	....	....	....	....	....	....	×	

[33] *Paramys murinus* (?Lost Cabin, Wind River Basin)—Princeton Museum collection.

[34] *Paramys buccatus* (Lysite, Wind River Basin)—Loomis, 1919, p. 217.

Paramys buccatus (Lost Cabin, Wind River Basin)—Princeton Museum collection.

[35] *Paramys* cf. *P. copei* (Huerfano A)—American Museum of Natural History collection.

[36] *Paramys major quadratus* (?Lysite, Big Horn Basin)—see note 49.

[37] *Paramys* sp. indet. (Clark Fork)—Van Houten, 1944, p. 180.

[38] *Sciuravus depressus* (Lysite, Wind River Basin)—This specimen "I judge not to be *Sciuravus* but a separate genus" (Troxell, 1923, p. 385).

[39] *Mysops kalicola* (Lost Cabin, Wind River Basin)—"cannot be assigned very well to Leidy's genus, neither is it referable to *Sciuravus* Marsh. It is probable as close to '*Paramys*' as to any other described form, but very likely represents an undescribed species" (Wilson, 1937, p. 455).

[40] *Thryptacodon antiquus* (?Lysite, Big Horn Basin)—American Museum of Natural History collection. Matthew, 1915a, p. 7, states that this genus has not been found in the Lysite or Lost Cabin.

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Protopsalis Cope, 1880											
tigrinus										×	
Palaeonictinae Denison, 1938											
Dipsalodon Jepsen, 1930											
matthewi	×										
Palaeonictis Blainville, 1842											
occidentalis			$\times^{M}_{L}$								
Ambloctonus Cope, 1875											
sinosus								?			
hyaenoides								×			
major									×		
Mesonychidae Cope, 1875											
Dissacus Cope, 1881											
praenuntius	×										
navajovius longaevus			$\times^{M}_{L}$								
Pachyaena Cope, 1874											
gigantea gigantea[41]			×								
gigantea ponderosa			×								
gracilis			×								
ossifraga			×	?				?			
cf. *Pachyaena*[42]		×			?				?		
Hapalodectes Matthew, 1909											
leptognathus			$\times^{U}_{?}$								
compressus					×	×				×	
sp.[43]											×
Hyaenodontidae Leidy, 1869											
Limnocyoninae Wortman, 1902											
Prolimnocyon Matthew, 1915											
robustus			$\times^{M}$								
atavus			$\times^{U}_{M}$	P?	?					×	
antiquus											
Proviverrinae Matthew, 1909											
Sinopa Leidy, 1871											
mordax			×								
opisthotoma			×								
shoshoniensis			×								
secundaria			P	?				?			
viverrina[44]			cf	?						cf	
strenua			×	?		P				×	
hians			×	×		×				?	
multicuspis			×	?	?					×	
vulpecula			×		P				×		
Tritemnodon Matthew, 1906											
whitiae									P	×	

[41] *Pachyaena gigantea gigantea*—Matthew, 1915a, p. 97, gives range Wasatch of Big Horn Basin. Hay, 1930, p. 468, has recorded it erroneously as Lower Eocene (Wasatch, Wind River?) Wyoming.

[42] Cf. *Pachyaena* (Indian Meadows formation)—Love, 1939, p. 63.

Cf. *Pachyaena* (?Lysite, ?Lost Cabin, Big Horn Basin—Matthew, 1915a, p. 88.

[43] *Hapalodectes* sp. (Huerfano A)—American Museum of Natural History collection.

[44] *Sinopa* cf. *S. viverrina* (Gray Bull)—Princeton Museum collection.

Sinopa cf. *S. viverrina* (Lost Cabin, Wind River Basin)—American Museum of Natural History collection.

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Miacidae Cope, 1880											
Viverravinae Matthew, 1909											
Didymictis Cope, 1875											
protenus proteus	×										
protenus curtidens[45]	....	....	$\times^{U}_{M}_{L}$								
protenus leptomylus	....	....	?								
protenus protenus	....	....	....	×	....	....	....	×			
altidens lysitensis	....	....	....	....	×	×					
altidens altidens[46]	....	....	....	....	....	....	cf	....	×	×	cf
Viverravus Marsh, 1872											
acutus[47]	....	....	$\times^{U}_{M}_{L}$	....	?cf	cf					
politus	....	....	$\times^{M}_{L}$								
dawkinsianus	....	....	....	....	....	×	....	....	....	×	×
Miacinae Trouessart, 1885											
Miacis Cope, 1872											
exiguus	....	....	$\times^{U}_{M}$								
latidens	....	....	$\times_{?L}$	....	....	....	....	....	....	×	
sp. indet.[48]	....	....	....	?	....	....	....	?			
Vassacyon Matthew, 1909											
promicrodon	....	....	$\times^{M}_{?L}$	....	....	....	....	....	....	P	
Uintacyon Leidy, 1871											
vorax	....	....	cf_{L}								
massetericus rudis	....	....	$\times^{?}_{L}$								
massetericus massetericus	....	....	$\times^{U}_{?L}$	×	×						
Vulpavus Marsh, 1871											
australis	....	....	$\times^{U}_{?M}$	?	×	....	....	×	....	×	
canavus	....	....	$\times^{U}$	....	....	×	....	....	....	×	
Condylarthra Cope, 1881											
Phenacodontidae Cope, 1881											
Phenacodus Cope, 1873											
primaevus primaevus[49]	P	....	×	×	?	....	×	....	....	×	

[45] *Didymictis protenus curtidens* (Gray Bull)—"If there are two subspecies . . . in the Gray Bull, *curtidens* applies to the larger animals" (Simpson, 1937b, p. 15).

[46] *Didymictis* cf. *D. altidens* (Huerfano A)—Osborn, 1909, p. 49 (=*D. leptomylus* in Osborn, 1929, p. 274).

[47] *Viverravus* cf. *V. acutus* (?Lysite, Big Horn Basin)—American Museum of Natural History collection.

Viverravus cf. *V. acutus* (Lysite, Wind River Basin)—Princeton Museum collection.

[48] *Miacis* sp. indet. (?Almagre, ?Largo)—Matthew 1915a, p. 36.

[49] *Phenacodus primaevus primaevus* (?Lysite, ?Lost Cabin, Big Horn Basin)—Loomis, 1907, pp. 357–362, lists *Esthonyx* sp., *Paramys quadratus*, *Phenacodus primaevus*, *Phenacodus vortmani*, *Hyracotherium cristatum*, *Heptodon posticus*, and *Lambdotherium primaevum* (diagnostic of Lost Cabin) from the Buffalo Basin level in the Big Horn Basin. Buffalo Basin is a local name for the upper Dry Cottonwood Creek drainage south of Tatman Mountain. If all the specimens were found at the same level they are Lost Cabin, but the available evidence suggests that most of the material was not associated with *Lambdotherium*.

In a columnar section of the Big Horn Basin Lower Eocene deposits compiled by Osborn (1910, p. 122) from Loomis' sections, *Hyracotherium cristatum* occurs with *Lambdotherium*. Granger, 1908, p. 239, recorded *H. cristatum* only from "Greybull River, Big Horn Basin, Wyo.," without referring to Loomis' specimen.

Granger, 1915, p. 354, reported that "no phenacodonts have been found in the Lost Cabin horizon of the Big Horn Basin. He did record *Phenacodus* (*P. copei*) from the Lysite of Buffalo Basin, but did not mention Loomis' specimens.

Matthew, 1918, p. 614, gives *Paramys major*

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
primaevus intermedius	....	....	×	P	....	....	....	....	....	P	
p., small var. cf. *intermedius*	×										
primaevus hemiconus	....	....	×	....	....	....	....	....	....	×	
robustus	....	....	×								
brachypternus	....	....	×	×	....	P	....	P			
astutus	....	....	....	?							
distans[50]	....	....	....	?	....	....	....	?			
sulcatus[51]	....	....	....	?	....	....	....	?			
copei[52]	....	....	×	×	×	×	....	....	....	×	
vortmani[53]	....	....	P	P	?	×	....	....	....	×	
sp.[54]	....	×	....	....	....	....	....	....	....	....	×
Ectocion[55] Cope, 1882											
parvus	×										
osbornianus ralstonensis	×										
osbornianus osbornianus	....	....	$\times^{\frac{I}{M}}_{L}$								
superstes	....	....	P_{rL}	....	....	....	....	....	....	×	
Meniscotheriidae Cope, 1882											
Meniscotheriinae Simpson, 1937											
Meniscotherium Cope, 1874											
tapiacitis	....	....	....	....	....	....	....	×			
chamense chamense	....	....	....	....	....	....	....	×	....	×	
chamense terraerubrae	....	....	....	....	....	....	....	×			
robustum	....	....	....	....	....	....	×				
? priscum[56]	×										
Hyopsodontidae Lydekker, 1889											
Hyopsodontinae Trouessart, 1879											
Haplomylus Granger, 1915											
speirianus	×	×	$\times^{M}_{L}$								

quadratus (*P. quadratus* of Loomis) probably from the Lost Cabin beds of Buffalo Basin, Wyoming, although it may be Lysite.

According to Osborn, 1929, p. 70, the type of *Heptodon posticus* is from the Lysite of the Big Horn Basin.

These data indicate that most of Loomis' material was probably found in Lysite beds in Buffalo Basin. This accords with the fact that Lysite beds are extensively exposed in Buffalo Basin, especially on the southern flank of Tatman Mountain. The specimens of *Lambdotherium* were recovered from the west end of Tatman Mountain (Granger, 1914, p. 202), and may have been mixed in collecting.

[50] *Phenacodus distans*—Incertae sedis; see Granger, 1915, pp. 347–348.

[51] *Phenacodus sulcatus*—Incertae sedis; see Granger, 1915, pp. 347–348.

[52] *Phenacodus copei* (Lost Cabin, Wind River Basin)—Princeton Museum collection.

[53] *Phenacodus vortmani* (?Lysite, Big Horn Basin)—see note 49.

[54] *Phenacodus* sp. (Huerfano A)—American Museum of Natural History collection.

[55] *Ectocion*—Cope, 1884, p. 696, recorded *Ectocion osbornianum*, but did not give the derivation of *Ectocion*. His diagnosis of the genus (p. 694) suggests that the word was derived from ἐκτὸς = outside, and κίων = column or pillar (m. or f.) meaning external cusp. *Ectocion* is therefore considered to be masculine.

[56] *Meniscotherium? priscum* (Clark Fork)—The type (and only) specimen cannot be found (Simpson, personal communication). There is some doubt that this species is referable to *Meniscotherium* in view of the fact that all its well-established species are later Wasatchian. Russell, 1929, p. 178, has described *Meniscotherium semicingulatum*, based on a right P^4 and a left P^3, from Upper Paleocene deposits of Canada. This seems to confirm the Paleocene occurrence of the genus, though, as yet, the Paleocene material is perhaps too poor to definitely establish the presence of *Meniscotherium*.

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Hyopsodus Leidy, 1870											
simplex	....	×	$\times^{?}_{L}$								
latidens	....	×									
miticulus	....	....	×	×							
powellianus powellianus[57]	....	....	?	....	×	×	....	....	cf	....	cf
powellianus browni	....	....	....	....	×	×	....	....	P		
wortmani minor	....	....	....	....	×	×	....	....			
wortmani wortmani[58]	....	cf	....	....	....	....	....	....	×	×	
mentalis mentalis	....	....	×	×	?	P	....	×	××	××	
mentalis lysitensis	....	....	....	P	×	×	....	....	××	××	
walcottianus	....	....	....	....	....	....	....	....	×	×	
sp.[59]	....	....	....	....	....	....	×				
?Hyopsodontidae											
Phenacodaptes Jepsen, 1930											
sp. indet.[60]	....	....	$\times_{L}$								
Pantodonta Cope, 1873											
Coryphodontidae Marsh, 1876											
Coryphodon Owen, 1845											
armatus	....	....	?	×	?	....	....	×			
cinctus	....	....	×								
curvicristis	....	....	×								
cuspidatus	....	....	×	×							
elephantopus	....	cf	×	×	?	....	×				
hamatus	....	....	×	....	....	....	×				
latidens	....	....	×	×	....	....	....	P			
labatus	....	....	×	×	?						
marginatus	....	....	×								
radians	....	....	×	×	....	....	×				
semicinctus	....	....	....	....	....	....	×				
singularis	....	....	....	....	....	....	....	....	....	×	
testis	....	....	×	×	....	....	....	....	....	×	cf
ventanus	....	....	....	....	....	....	....	....	....	×	
wortmani	....	....	....	....	....	....	....	....	....	×	
sp. nov.[61]	×	....	$\times^{M}$								
Dinocerata Marsh, 1873											
Uintatheriidae Flower, 1876											
Probathyopsis Simpson, 1929											
praecursor	×	....	$?_{L}$								
successor	....	....	$\times_{L}$								
sp. nov.[62]	×										
Bathyopsis Cope, 1881											
fissidens[63]	....	....	....	....	....	....	....	....	....	×	

[57] *Hyopsodus* cf. *H. powellianus* (Lost Cabin, Big Horn Basin)—Sinclair and Granger, 1911, p. 108.

Hyopsodus cf. *H. powellianus* (Huerfano A)—Osborn, 1897, p. 256.

[58] *Hyopsodus* cf. *H. wortmani* (Indian Meadows formation)—Love, 1939, p. 63.

[59] *Hyopsodus* sp. (Knight formation)—Granger, 1914, p. 203.

[60] *Phenacodaptes* sp. indet. (lower Gray Bull)—Princeton Museum collection.

[61] *Coryphodon* sp. nov. (Clark Fork)—Princeton Museum collection.

Coryphodon sp. nov. (middle Gray Bull)—Princeton Museum collection.

[62] *Probathyopsis* sp. nov. (Clark Fork)—Jepsen, 1930a, p. 129.

[63] *Bathyopsis fissidens*—Cope, 1884, p. 600, records a specimen from the Big Horn badlands, which is American Museum of Natural History catalogue No. 4821. Card states "Wortman doubts correctness of this record, thinks the specimen was Wind River."

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Notoungulata Roth, 1903											
Arctostylopidae Schlosser, 1923											
Arctostylops Matthew, 1915											
steini	....	....	$\times_L$								
Perissodactyla Owen, 1848											
Equidae Gray, 1821											
Hyracotheriinae Cope, 1881											
Hyracotherium Owen, 1840											
cristatum[64]	....	....	×	....	?	....	....	....	?		
etsagicum	....	×	×								
montanum	....	....	×								
resartum	....	....	×								
angustidens	....	....	....	?	....	....	....	?			
cristonense	....	....	P	?	....	....	....	?			
validum	....	....	....	?	....	....	....	?			
boreale	....	....	×	....	....	×	....	....	....	×	
index	....	....	×	?	....	....	×	?			
vasacciense	....	....	....	....	....	....	×				
craspedotum	....	....	....	....	....	×	....	....	....	×	
venticolum	....	....	....	....	....	....	....	....	....	×	
sp.[65]	....	....	....	×	×	....	....	×	×	....	×
Brontotheriidae Marsh, 1873											
Lambdotheriinae Hay, 1902											
Lambdotherium Cope, 1880											
primaevum[66]	....	....	....	....	....	....	....	....	×		
popoagicum[67]	....	....	....	....	....	....	×	....	×	×	×
priscum	....	....	....	....	....	....	....	....	....	×	×
progressum	....	....	....	....	....	....	....	....	....	×	×
magnum	....	....	....	....	....	....	....	....	×	....	×
Palaeosyopinae Steinmann & Döderlein, 1890											
Eotitanops Osborn, 1907											
borealis	....	....	....	....	....	....	....	....	....	×	
major	....	....	....	....	....	....	....	....	....	×	
princeps	....	....	....	....	....	....	....	....	....	×	
brownianus	....	....	....	....	....	....	....	....	....	×	?
gregoryi	....	....	....	....	....	....	....	....	....	×	
Isectolophidae Peterson, 1919											
Homogalaxinae Peterson, 1919											
Homogalax[68] Hay, 1899											
primaevus	....	....	×								
protapirinus	....	....	×								
semihians	....	....	×								

[64] *Hyracotherium cristatum*—see note 49.

[65] *Hyracotherium* sp. (Huerfano A)—Osborn, 1909, p. 49.

[66] *Lambdotherium primaevum*—Sinclair and Granger, 1911, p. 108, refer this species to *L. popoagicum*. Osborn, 1929, p. 282, considers it distinct.

[67] *Lambdotherium popoagicum*—Hay, 1930, p. 711, erroneously gives range Lower Eocene of New Mexico. Hay, 1902, p. 629, correctly records Wyoming and Colorado. Bonillas, 1936, revised the genus, considering this the only valid species to which all specimens of *Lambdotherium* should be referred.

[68] *Homogalax*—Troxell, 1922, described *Homogalax* from Bridger and Uinta deposits. Dr. H. E. Wood, II (personal communication) states "I consider Troxell's '*Homogalax bridgerensis*' as referable to *Isectolophus latidens*, and his '*Homogalax uintensis*' as referable to *Schizolophodon*, and inseparable from *cuspidens*."

TABLE IV.—*Continued*

	Clark Fork	Indian Meadows formation	Gray Bull	Almagre	Lysite, Big Horn Basin	Lysite, Wind River Basin	Knight formation	Largo	Lost Cabin, Big Horn Basin	Lost Cabin, Wind River Basin	Huerfano A
Helaletidae Osborn, 1892											
Helaletinae Wortman & Earle, 1893											
Heptodon Cope, 1882											
calciculus										×	
posticus[69]					×				?		
ventorum						×			×	×	
brownorum										×	
sp.[70]							×				×
Hyrachyidae Wood, 1927											
Hyrachyus Leidy, 1871											
modestus										cf	
Artiodactyla Owen, 1847											
Dichobunidae Gill, 1872											
Dichobuninae Zittel, 1893											
Bunophorus Sinclair, 1914											
etsagicus[71]			×							×	
macropternus[72]			?		?	×			?		
Wasatchia Sinclair, 1914											
grangeri			$\times^{U}$								
dorseyana			$\times^{U}_{M}$					×			
lysitensis					×	×					
Diacodexis Cope, 1882											
laticuneus			×								
robustus			×		?						
chacensis[73]		×	×	?	×			?		×	
nuptus[74]			?								
secans										×	
olseni										×	
sp.[75]							×	×			×
Choeropotamidae Owen, 1845											
Parahyus[76] Marsh, 1876											
aberrans	Early Eocene, Washakie Basin										
vagus	Early Eocene, Washakie Basin										

[69] *Heptodon posticus*—see note 49.

[70] *Heptodon* sp. (Knight formation; Huerfano A)—American Museum of Natural History collection.

[71] *Bunophorus etsagicus* (Lost Cabin, Wind River Basin)—Princeton Museum collection.

[72] *Bunophorus macropternus* (Lysite, Wind River Basin)—Princeton Museum collection.

[73] *Diacodexis chacensis*—Sinclair, 1914, p. 290, refers *D. metsiacus* and *D. brachystomus* to this species. Matthew, 1909, p. 95, gives range Wasatch of New Mexico.

Diacodexis chacensis (Indian Meadows formation)—Love, 1939, p. 63.

Diacodexis chacensis (Lost Cabin, Wind River Basin)—Princeton Museum collection.

[74] *Diacodexis nuptus*—Hay, 1930, p. 756, gives range Lower Eocene (Wind River), Wyoming, Colorado, but cites no source later than Matthew, 1909, p. 95, who reports range Wasatch, Big Horn Valley, Wyoming.

[75] *Diacodexis* sp. (Knight formation; Largo)—American Museum of Natural History collection.

Diacodexis sp. (Huerfano A)—American Museum of Natural History collection. Osborn, 1909, p. 49, called it *Trigonolestes* sp.

[76] *Parahyus*—Sinclair, 1914, p. 290, wrote: "Marsh states that [the species] are from the *Coryphodon* beds of Wyoming. Hay's catalogue locates them in the Bridger, while Matthew's checklist [1902] gives the locality as *Coryphodon* zone, Black Buttes, Washakie Basin, Wyoming. Professor R. S. Lull kindly informs me that the type of *P. vagus*, catalogue No. 10972 Yale University Museum, comes from Bitter Creek station, Wyoming [northwest margin of Washakie Basin]. *P. aberrans*, catalogue No. 10027, was shipped from Fort Bridger, Wyoming, and this is the only record regarding its geographic locality." Matthew (1909, p. 95) gave range Wasatch Lower Eocene.

bicuspis (Loomis, 1907b, p. 357; species is listed but not described), *Anaptomorphus minimus* (Loomis, 1906, p. 278. Matthew, 1918, p. 604, refers this specimen to *?Nyctitherium celatum.* Simpson, 1940,p. 208, nevertheless, indicates presence of *Anaptomorphus* questionably in Early Eocene).

Lysite beds, Wind River Basin: *Notharctus, Notharctus venticolus* (Loomis, 1919, p. 217, no description or discussion).

Lost Cabin beds, Wind River Basin: *Pelycodus, Paramys delicatior, ?Helohyus, ?Wasatchia.*

Huerfano A: *Pelycodus, ?Omomys, ?Wasatchia.*

Knight formation: *Homacodon priscus* and *H. pucillus* (Sinclair, 1914, pp. 284–286, revised the genus but discussed no Early Eocene species. Marsh, 1894, p. 261, records these species from *Coryphodon* beds of Wyoming and New Mexico, based on astragali only), *Entomacodon minutus* (Hay, 1930, p. 435, erroneously records range as Early Eocene, Wasatch, Wyoming. He cites no reference later than Matthew, 1909, p. 96, who gives Lower Bridger).

Almagre or Largo beds: *Periptychus* sp. (Granger, 1915, p. 347, "*Eohyus robustus*, from 'Lower Eocene of New Mexico' a type which Sinclair has correctly referred to *Periptychus*, a Torrejon genus." Presumably from Torrejon beds of New Mexico), *Heptodon singularis* (in Hay, 1930, p. 724. Matthew, 1909, p. 94, states that the species is incertae sedis), *Homacodon priscus* and *H. pucillus* (Marsh, 1894, p. 261; based on astragali only, other remains of these species are not distinctive), *Sarcolemur crassus* (Cope, 1877, p. 149; based on first and second right lower molar. Reference of this specimen to *Sarcolemur* is very questionable).

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NEW UPPER CAMBRIAN TRILOBITES FROM THE LÉVIS CONGLOMERATE

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ABSTRACT.—The present paper is intended as a supplement to a previous one on the Upper Cambrian trilobites from the Lévis conglomerate. Twenty-seven new species and seven genera are described and illustrated.

More detailed descriptions and new illustrations are also presented for a few of the previously known species. All the species discussed belong to the late Upper Cambrian *Hungaia magnifica* zone.

INTRODUCTION

IN AN EARLIER paper (Rasetti, 1944) on the Upper Cambrian trilobites from the Lévis conglomerate, the writer dealt with all the previously known species, and described 45 new ones. In the relatively short time since the previous paper was completed, a considerable amount of new material has become available. The late Dr. Charles E. Resser asked the writer to study the large collection of Upper Cambrian trilobites from the locality (over 1500 specimens), which had been assembled by Dr. E. O. Ulrich in connection with his studies on the Ozarkian system. In the meantime, the writer's own collecting had supplied new material. All together, there are now 27 new species and a number of unassigned pygidia which are deemed worthy of description. This does not include many trilobites that do not appear to belong to any described species or even genus. Their description has been omitted as they are not represented by sufficiently complete or well-preserved specimens.

The writer believes that publication of the new species and genera will be of help to students of late Upper Cambrian faunas, especially those from the Cordilleran province. The knowledge of Trempealeau faunas —if we except the excellent monographs on the Dikelocephalinae and Saukiinae by Ulrich and Resser—has lagged behind that of the Dresbach and Franconia faunas, on which much progress has recently been made through the work of Resser, Lochman, Duncan and others.

An additional reason for publication at the present time is that new material from the locality in question is not likely to turn up in the near future. As far as the writer knows, there are no important unstudied collections extant. New collecting may occasionally supply a few new forms, but the outcrops have now been so thoroughly and systematically explored that important discoveries are unlikely.

The writer wishes to express his great indebtedness to the late Dr. Charles E. Resser and to Dr. G. Arthur Cooper for making available the trilobites from the collections of the U. S. National Museum. He also wishes to express heartfelt thanks to Mr. Hubert Lechevalier for his effective help with the collection of the fossils.

FAUNAL ASSOCIATIONS

The questions regarding the age of the Lévis faunas were discussed in the previous paper, and there is no need for repetition here. All the new species whose faunal associations are known belong to the *Hungaia magnifica* zone, and most of the others can be safely assumed to be of the same age because of their affinity with known species. One doubtful case will be discussed in the systematic descriptions.

Most of the material in the U.S.N.M. collections is segregated according to the boulder from which the specimens were recovered. Part of these boulders were collected by R. Bell, of the Geological Survey of Canada, in 1860. The boulders in the U.S.N.M. are designated as A-1, A-2, A-3, and A-4. The locality is probably on North Ridge, since the early collectors do not seem to have secured Upper Cambrian fossils from other outcrops. Some of the material

in the U.S.N.M. is not assigned to any particular boulder.

Since faunal associations are of great importance, all the species identified in the four boulders represented in the U.S.N.M. collections, and in a few additional boulders collected by the writer, are listed in the accompanying table.

SYSTEMATIC DESCRIPTIONS

ORDER AGNOSTIA

Genus LOTAGNOSTUS Whitehouse, 1936

LOTAGNOSTUS cf. L. TRISECTUS (Salter)

Plate 60, figure 1

Agnostus trisectus SALTER, 1864, Geol. Survey Mem., British Organic Remains, dec. 11, pt. 1, p. 10, pl. 1, fig. 11.

Lotagnostus trisectus, WHITEHOUSE, 1936, Queensland Mus. Mem., vol. 11, pt. 1, p. 101.

A single pygidium closely resembles this European species; however, the material is considered insufficient for a positive specific identification. Raymond (1924) reported a similar specimen from the Gorge. These finds are interesting, in view of the small number of species in these faunas that present European affinities.

Boulder 15, North Ridge. Laval Univ. no. 1102.

MISCELLANEOUS TRILOBITES

Genus ACHEILUS Raymond, 1924

ACHEILUS SPINOSUS Rasetti, n. sp.

Plate 60, figure 2

This species resembles *A. latus* Rasetti in general proportions and convexity of the cranidium. Glabella relatively short and wide, expanding forward, moderately convex; two pairs of glabellar furrows faintly impressed. Palpebral lobes relatively large for the genus. Occipital segment bearing a sharply pointed spine. The last-mentioned character distinguishes this form from most of the described species. Length of holotype cranidium 3.5 mm.

Lévis, probably from North Ridge (boulder A-1). Holotype, U.S.N.M. no. 111719.

ACHEILUS CONVEXUS Rasetti, n. sp.

Plate 60, figures 3–7

This form resembles the genotype, *A. marcoui* Raymond, more than any other described species. In both species, the glabella is strongly convex in longitudinal section, so that the anterior part is not visible from above. The glabella expands forwards, and is proportionately wider and shorter than in *A. marcoui;* only the furrows of the posterior pair are well impressed. The occipital segment is narrow and simple. The palpebral lobes are smaller and closer to the glabella than in *A. marcoui;* the posterolateral limbs are shorter than in that species and droop at a steep angle. The glabella has a punctate surface.

The pygidium does not possess an axial spine. The axis is strongly convex and almost reaches the posterior margin. The pleural lobes, as in other species of the genus, are narrow and steeply inclined. The axis shows two furrows, and the pleural lobes two pairs of faint furrows and grooves. Surface characters same as those of cranidium.

Length of largest cranidium 4.5 mm.; of pygidium 2 mm.

Boulder 60, South Ridge. Holotype and paratypes, Laval Univ. nos. 1173 a-i.

ACHEILUS TRIANGULARIS Rasetti, n. sp.

Plate 60, figure 8

This species belongs to the group of *A. communis* Rasetti. Compared with that species, the glabella is proportionately narrower and longer. The main distinctive character, however, lies in the occipital segment, which forms a sharply triangular spine.

The surface of the cranidium is covered with irregular ridges, which assume a transverse course on the anterior portion of the glabella.

Length of holotype cranidium 2 mm.

Boulder 15, North Ridge. Holotype, Laval Univ. no. 1174.

ACHEILUS? MARGINATUS Rasetti, n. sp.

Plate 60, figures 9–13

This species is not typical of the genus in one respect, *i.e.*, in possessing a narrow, wirelike rim in front of the glabella. Nevertheless, since such forms as *A. communis* and *A. limbatus* connect it with the more typical species of *Acheilus*, there is no doubt in the writer's mind that all these trilobites are closely related. It is possible that the present species should be referred to *Triarthropsis*. However, suspecting that the common characters may be indicative of parallel development rather than real affinity, the writer prefers to assign the species to *Acheilus*. It

TABLE 1.—FAUNAL ASSOCIATIONS IN THE UPPER CAMBRIAN BOULDERS

Boulder	A-1	A-2	A-3	A-4	14	57	59	60	61
Acheilus convexus Rasetti								×	
Acheilus gibbus Rasetti	×								
Acheilus latus Rasetti	×								
Agnostus americanus Billings			×						
Agnostus orion Billings			×						
Apatokephaloides pauper (Billings)		×	×			×			
Apatokephaloides rotundatus Rasetti	×								
Aposolenopleura carinata Rasetti		×	×			×	×		
Bayfieldia tumifrons Clark		×	×	×		×			
Bayfieldia ulrichi Rasetti	×								
Bellaspidella minor Rasetti						×			
Bellaspidella? latifrons Rasetti			×	×					
Bellaspis billingsi Rasetti								×	
Bellaspis? granulata Rasetti								×	
Bellaspis? tuberculata Rasetti									×
Bienvillia corax (Billings)		×					×		
Glyptometopus laflammei (Clark)			×						
Hungaia magnifica (Billings)		×		×		×			
Keithia similis Rasetti	×								
Keithia subclavata (Billings)		×	×			×			
Keithiella cylindrica (Billings)	×	×	×			×			
Lauzonella planifrons (Billings)		×	×	×					
Lecanopyge? billingsi (Clark)		×	×			×			
Leiocoryphe brevis (Raymond)	×								
Leiocoryphe gemma Clark						×			
Leiocoryphe transversa Rasetti	×				×	×			
Levisella brevifrons Rasetti								×	
Levisella oweni (Billings)		×	×	×					
Litagnostus levisensis Rasetti			×						
Loganellus belli (Billings)		×	×	×					
Loganellus logani (Devine)				×					
Loganellus similis Rasetti							×		
Loganopeltoides zenkeri (Billings)		×				×			
Onchonotus convexus Rasetti	×								
Onchonotus globosus (Billings)		×	×	×					
Onchonotus nasutus (Walcott)		×	×	×		×			
Onchonotus richardsoni (Walcott)				×					
Onchonotus sulcatus Rasetti	×		×			×			
Onchonotus? sedgwicki (Billings)		×	×	×					
Parabolina? incerta Rasetti			×						
Paranorwoodia venusta Rasetti						×			
Phoreotropis? marginata Rasetti		×							
Platycolpus capax (Billings)		×				×			
Platycolpus dubius (Billings)		×							
Platydiamesus depressus Raymond	×								
Platydiamesus levisensis Rasetti			×			×			
Plethometopus acutus Rasetti					×				×
Plethometopus armatus (Billings)		×	×					×	
Plethometopus laevis (Raymond)					×				
Plethometopus obtusus Rasetti						×			
Pseudagnostus canadensis (Billings)			×		×	×			
Pseudagnostus gyps (Clark)			×					×	
Pseudosaukia brevifrons (Clark)			×		×				×
Resseraspis carinata Rasetti								×	
Richardsonella convexa Rasetti			×						
Richardsonella cristata (Billings)		×	×			×			
Richardsonella megalops (Billings)		×	×						
Stenopilus elongatus Rasetti	×								
Stenopilus intermedius Clark						×			
Stigmametopus levisensis Rasetti	×								
Taenicephalina lechevalieri Rasetti								×	
Tatonaspis levisensis Rasetti		×	×	×		×	×		
Westonaspis laevifrons Rasetti					×				

must be added that the libragenes and pygidium are typical of the latter genus.

Glabella parallel-sided, regularly rounded in front, moderately convex. Two pairs of faint glabellar furrows, the posterior ones sharply turned backwards as in typical forms of *Acheilus*. Occipital segment expanded and bearing a small tubercle. Palpebral lobes of the same size and position as in *A. marcoui*. Surface finely granulose.

Libragenes with a striated rim not defined by a furrow, and short genal spines.

Pygidium with a large convex axis showing four faint furrows, and narrow inclined pleural lobes. Two pairs of pleural furrows and grooves are present.

Length of largest cranidium 4.5 mm., of pygidium 2 mm.

Boulder 39, North Ridge. Holotype and paratypes, Laval Univ. nos. 1175 a-d.

Genus APATOKEPHALOIDES Raymond, 1924

APATOKEPHALOIDES PAUPER (Billings)

Plate 60, figure 14

Dikelocephalus pauper BILLINGS, 1865, Canada Geol. Survey, Paleozoic fossils, vol. 1, p. 200.
Ptychaspis? pauper, WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, p. 352.
Apatokephaloides pauper, RASETTI, 1944, Jour. Paleontology, vol. 18, no. 3, p. 238, pl. 36, figs. 42–43.

The previously illustrated cranidia are all exfoliated. A specimen preserving the test is figured, in order to show the finely granulated surface.

The figured plesiotype is from boulder 57, North Ridge.

APATOKEPHALOIDES ROTUNDATUS Rasetti, n. sp.

Plate 60, figures 15, 16

In this species the glabella is proportionately shorter and wider than in *A. pauper*, and even more so than in *A. inflatus* Raymond. The anterior outline of the glabella is more regularly rounded than in other species of the genus. Two pairs of glabellar furrows are faintly impressed. Other characters are as in *A. pauper*. Length of holotype cranidium 5 mm.

Boulder A-1, probably from North Ridge. Holotype and paratype, U.S.N.M. nos. 111700, 111701.

Genus BAYFIELDIA Clark, 1924

BAYFIELDIA ULRICHI Rasetti, n. sp.

Plate 60, figures 17–19

The cranidium of this species differs from that of *B. tumifrons* Clark in several respects. The glabella is proportionately longer and narrower, and the brim is somewhat narrower. The glabellar furrows are hardly impressed, as in *B. tumifrons*. The palpebral lobes are considerably larger than in Clark's species, and are strongly rimmed. The occipital furrow is almost straight, instead of being sharply bent forward at the sides as in *B. tumifrons*. The surface is covered with prominent rounded tubercles. Although all the available specimens of *B. tumifrons* are exfoliated, fragments of test examined indicate that Clark's species is not so strongly tuberculated as the new one. The posterolateral limbs are narrow, as in *B. tumifrons*. Length of holotype cranidium 6 mm.

The associated pygidium has a prominent axis reaching the posterior margin and showing only one well-impressed furrow. The pleural lobes present two pairs of moderately impressed furrows and end in four pairs of short spines. The surface is tuberculated as that of the cranidium.

This pygidium appears to be identical with the one that Raymond assigned to *Apatokephaloides clivosus*. The writer believes that the present assignment is more likely to be correct, since Raymond himself states that his pygidium is tuberculated, whereas the cranidium of *A. clivosus* is almost smooth. Moreover, the shape of this pygidium agrees with other known pygidia of *Bayfieldia* and of the similar genera *Corbinia* and *Eurekia*.

Boulder A-1, probably from North Ridge. Holotype and paratypes, U.S.N.M. nos. 111702, 111703, 111703 a-c.

Genus BELLASPIDELLA Rasetti, n. gen.

Small trilobites known from the cranidium. Glabella moderately or rather strongly convex, tapering, rounded in front, with two pairs of rather well impressed furrows. Occipital furrow deep, occipital segment simple. Brim narrow, divided into a preglabellar area and a sharply upturned rim. Fixigenes narrow; anterior facial su-

tures slightly divergent. Palpebral lobes wide, about one-third the glabellar length; their centers situated back of the glabellar midpoint. Posterolateral limbs narrow.

Genotype, *B. resseri* Rasetti, n. sp.

Remarks.—The genus is erected for a few small forms which the writer has been unable to assign to any described genus, notwithstanding their resemblance to a number of other trilobites of the *Hungaia* zone. The name is meant to express the general resemblance to *Bellaspis*, from which *Bellaspidella* chiefly differs in the size and position of the palpebral lobes.

BELLASPIDELLA RESSERI Rasetti, n. sp.
Plate 60, figures 20–22

Glabella strongly convex in both directions, tapering, rounded in front. Two pairs of glabellar furrows; the posterior ones deeply impressed, strongly oblique, reaching one-third of the glabellar width; furrows of other pair much shallower, shorter and slightly oblique. Fixigenes about one-fourth the glabellar width; anterior facial sutures slightly divergent. Preglabellar area narrow; rim wider than preglabellar area, almost flat, upturned, transversely striated, slightly pointed at the center. Palpebral lobes wide, flat, upturned, separated from the fixigenes by shallow furrows. Ocular ridges narrow, weakly elevated. Occipital furrow deep, straight; occipital segment of moderate width. Surface of test finely granulated. Length of holotype cranidium 4 mm.

Boulder A-2, probably from North Ridge. Holotype and paratypes, U.S.N.M. nos. 111704, 111705, 111705a, 111706, 111706a.

BELLASPIDELLA MINOR Rasetti, n. sp.
Plate 60, figures 23, 24

Glabella moderately convex; two pairs of glabellar furrows, about equally impressed and moderately oblique. Preglabellar area exceedingly narrow; rim strongly upturned, narrow, straighter than in *B. resseri*. Anterior angles of the cranidium rather strongly turned downward. Fixigenes about as wide as in *B. resseri;* palpebral lobes large, strongly curved. Occipital furrow straight; occipital segment moderately expanded at the center.

Notwithstanding the somewhat different proportions of the various cranidial parts, the species may be assigned to *Bellaspidella* on account of the size and shape of the palpebral lobes.

Surface faintly granulated. Length of holotype cranidium 2 mm.

Boulder 57, North Ridge. Holotype and paratype, Laval U. nos. 1177a-b.

BELLASPIDELLA? LATIFRONS Rasetti, n. sp.
Plate 60, figures 25–27

This species is assigned to the genus with some doubt, since the palpebral lobes are not preserved in any of the available specimens.

Glabella moderately convex, tapering, regularly rounded in front. Two pairs of very short glabellar furrows are well impressed; a third pair is visible on some of the specimens. Brim wider than in *B. resseri;* anterior facial sutures more widely divergent. Fixigenes and preglabellar area convex; rim wide, curved, strongly upturned. Palpebral lobes and posterolateral limbs not preserved. Surface smooth. Length of holotype cranidium 2 mm.

Boulder A-3, probably from North Ridge. Holotype and paratypes, U.S.N.M. nos. 111707, 111708, 111708a.

Genus BELLASPIS Rasetti, n. gen.

Small trilobites known from the cranidium. Glabella rather strongly convex, tapering, well defined by the dorsal furrows. Glabellar furrows weakly impressed; occipital furrow deep, occipital segment simple. Fixigenes about one-fourth the width of the glabella; palpebral lobes of average size, opposite the glabellar midpoint. Brim of moderate width, divided into a narrow, convex preglabellar area and a strongly elevated rim. Anterior facial sutures slightly divergent; the uniform width of the rim suggests that the suture remains marginal for a considerable distance. Posterolateral limbs of average size and shape.

Genotype, *B. billingsi* Rasetti, n. sp.

Remarks.—This genus is erected for a small form that is difficult to characterize, as it shares with a number of other genera the generalized trilobite features. Earlier paleontologists would have assigned any trilobite of this type to *Ptychoparia* or *Solenopleura*.

Among the genera of the *Hungaia* zone,

Taenicephalina somewhat resembles the present genus, but differs in the lesser convexity and prominence of the glabella, wider fixigenes, and the uneven width of the rim. *Aposolenopleura* has some features in common, but differs in the wider, much more convex fixigenes, strongly arched rim, and less impressed anterior furrow. The nearest genus is probably *Bellaspidella*.

The genus is named in honor of R. Bell, who collected many of the fossils described in this paper.

BELLASPIS BILLINGSI Rasetti, n. sp.
Plate 60, figures 34–36

Glabella moderately tapering, almost straight-sided, rounded in front. Two pairs of weakly impressed glabellar furrows. Occipital furrow deep; occipital segment somewhat elevated and expanded in the middle. Fixigenes narrow; palpebral lobes almost one-third the length of the glabella, faintly rimmed. Anterior facial sutures slightly divergent and straight to the anterior margin. Preglabellar area and rim of equal width, the latter strongly elevated, convex. Surface of test smooth. Length of largest cranidium 6 mm.

Boulder 60, South Ridge. Holotype and paratypes, Laval Univ. nos. 1178a-f.

BELLASPIS? TUBERCULATA Rasetti, n. sp.
Plate 60, figures 30, 31

This and the two following species are tentatively assigned to *Bellaspis* although it is by no means certain that this is their true generic position. Their chief distinctive character is the more prominent and strongly convex glabella.

Glabella tapering, highly arched in both directions, rising high above the fixigenes. Glabellar furrows exceedingly faint; occipital furrow deep, occipital segment relatively less elevated than in *B. billingsi*. Fixigenes about one-third the glabellar width, convex. Palpebral lobes not well preserved, but probably smaller than in the genotype; ocular ridges indistinct. Brim arched transversely, divided into a strongly convex rim and a somewhat wider preglabellar area. Anterior facial sutures scarcely divergent.

The surface of the test shows a few scattered tubercles, four pairs of which are symmetrically arranged on the glabella. Length of holotype cranidium 4 mm.

Boulder 61, South Ridge. Holotype and paratype, Laval Univ. nos. 1179a-b.

BELLASPIS? GRANULATA Rasetti, n. sp.
Plate 60, figures 28, 29

This species may best be compared with *B.? tuberculata*. Glabella, including the character of the glabellar furrows, occipital segment and furrow as in the preceding species. Fixigenes about one-fourth the glabellar width; palpebral lobes narrow, separated by a distinct furrow. Brim narrow; rim sharply upturned, but narrower and less elevated than in *B.? tuberculata* and in the other species assigned to the genus.

Surface of test finely granulated. Length of holotype cranidium 3 mm.

Boulder 60, South Ridge. Holotype and paratypes, Laval Univ. nos. 1182a-e.

BELLASPIS? ULRICHI Rasetti, n. sp.
Plate 60, figures 32, 33

Glabella strongly convex; glabellar furrows of the same shape as in the genotype, but more strongly impressed. Fixigenes about one-third the glabellar width, crossed by narrow, distinct ocular ridges that extend into the equally narrow palpebral lobes. Anterior facial sutures more strongly divergent than in *B. billingsi*. Preglabellar area and rim of about equal width; the latter sharply upturned, moderately convex. Posterolateral limbs and occipital furrow as in *B. billingsi*. Occipital segment strongly elevated in the middle.

Surface of test smooth. Length of holotype cranidium 4 mm.

Lévis, probably from North Ridge (boulder unknown). Holotype, U.S.N.M. no. 111718.

Genus GLYPTOMETOPUS Rasetti, 1944
GLYPTOMETOPUS LAFLAMMEI (Clark)
Plate 61, figures 1, 2

Solenopleura laflammei CLARK, 1924, Bull. Am. Paleontology, vol. 10, no. 41, p. 26, pl. 3, fig. 7.
Glyptometopus laflammei, RASETTI, 1944, Jour. Paleontology, vol. 18, p. 241, pl. 36, fig. 53.

A cranidium of this rare species was discovered in the U.S.N.M. collections and is figured as it shows certain details more clearly than the holotype.

Boulder A-3, probably from North Ridge. Plesiotype, U.S.N.M. no. 111728.

Genus KEITHIA Raymond, 1924
KEITHIA CONNEXA Rasetti, n. sp.
Plate 61, figures 3–5

The respective genotypes of *Keithia* and *Keithiella*, *Keithia schucherti* and *Keithiella cylindrica*, are trilobites of considerably different aspect. However, when more species became available, it appeared that these extreme forms were bridged by an almost continuous series, so that the limit between the two genera must be set arbitrarily.

In typical *Keithia* the rim is very narrow, and the tumid anterior part of the glabella overhangs it, so that the rim itself is not visible from above. The fixigenes in front of the eyes maintain an about even width, but they are so strongly folded downward that the sutures appear to converge when the cranidium is viewed from above. In typical *Keithiella* the cylindrical glabella has less convexity, leaving the wide rim well visible. The sutures diverge in front of the eyes, and this character is well apparent even when the cranidium is seen from above.

The species *Keithia schucherti* Raymond, *K. similis* Rasetti, *K. subclavata* (Billings), and the one being described, present a regular change in shape that is continued in *Keithiella maior* (to be described), *K. depressa* Rasetti, and *K. cylindrica* (Billings).

The present species may best be compared with *K. subclavata* (Billings). It differs in the wider rim and the uninterrupted posterior glabellar furrows. All the available specimens are exfoliated and show a faintly granular surface. Length of holotype cranidium 7 mm.

Lévis conglomerate, probably from North Ridge. Holotype and paratypes, U.S.N.M. nos. 111709, 111710, 111710a-c.

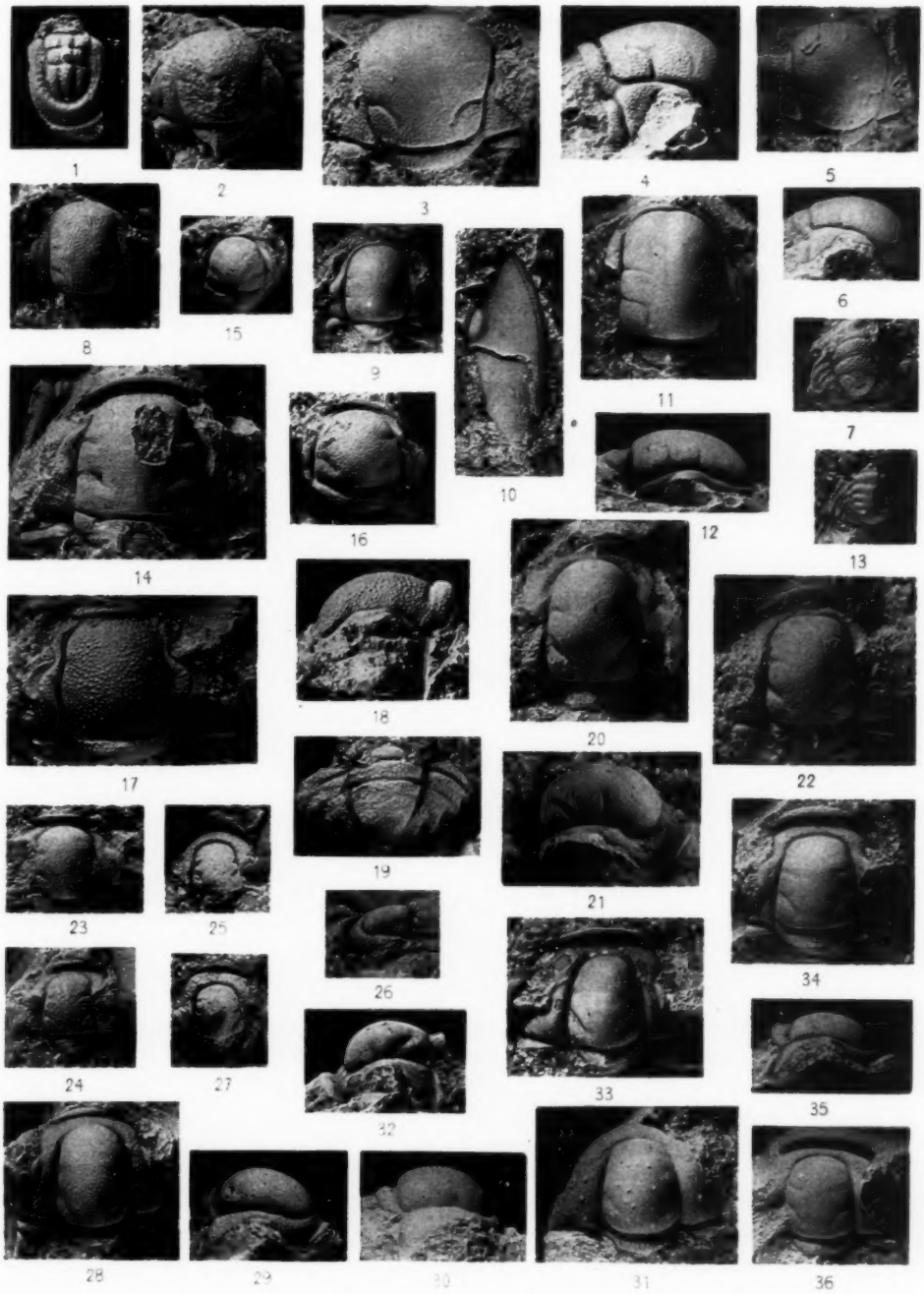
Genus KEITHIELLA Rasetti, 1944
KEITHIELLA MAIOR Rasetti, n. sp.
Plate 61, figures 6, 7

The chief characters that distinguish this species from the preceding are the less tumid anterior portion of the cranidium and the wider rim. Hence the cranidium, viewed from above, assumes the more quadrate shape characteristic of *Keithiella*. The posterior glabellar furrow of uniform depth across the glabella is also typical of the genus.

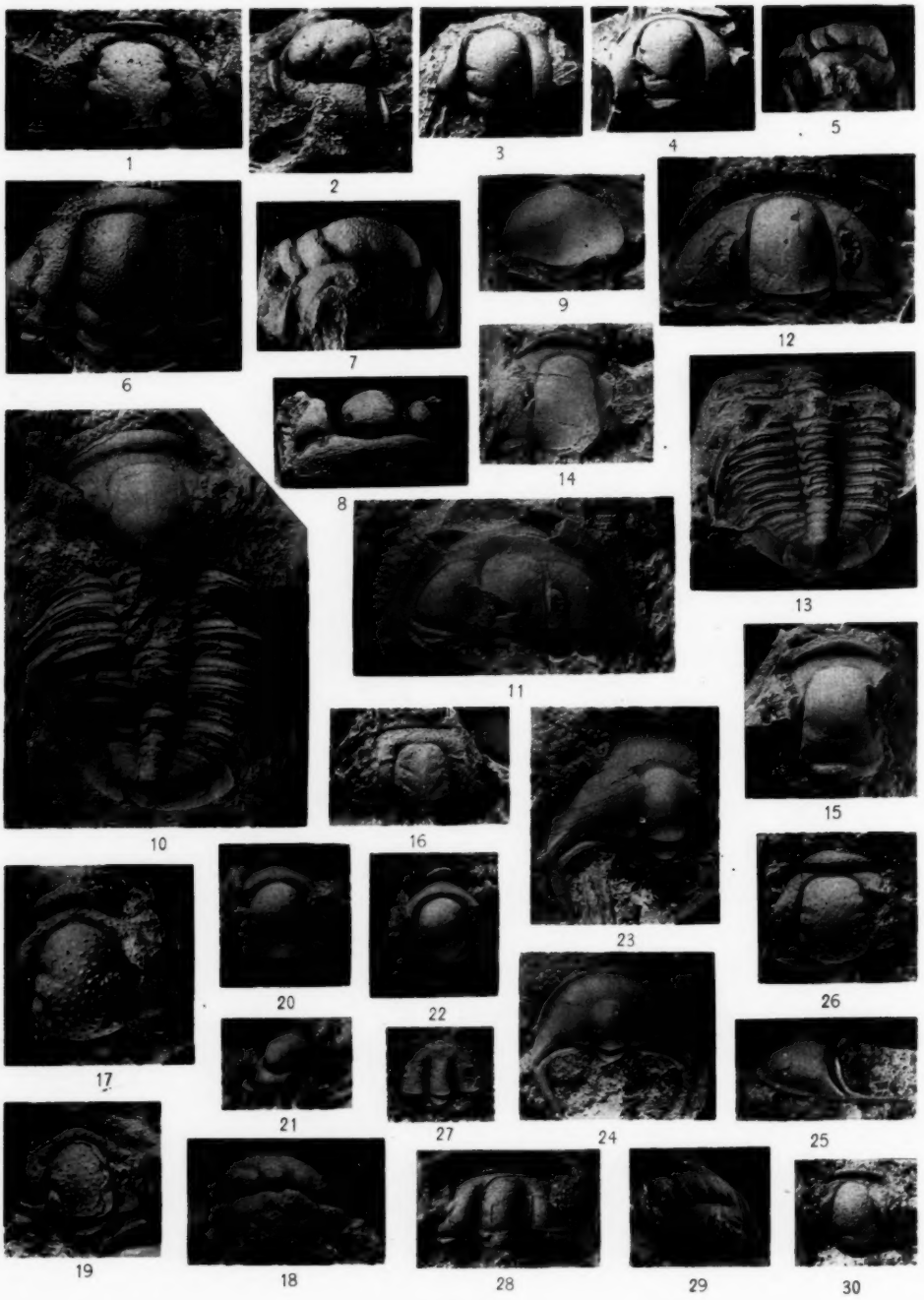
The anterior facial sutures appear to di-

EXPLANATION OF PLATE 60

FIGS. *1*—*Lotagnostus* cf. *L. trisectus* (Salter). Pygidium, ×5; Laval U. 1172. (p. 463)
2—*Acheilus spinosus* Rasetti, n. sp. Cranidium, ×5; U.S.N.M. 111719, holotype. (p. 463)
3–7—*Acheilus convexus* Rasetti, n. sp., ×5. *3*, *4*, Top and side views of cranidium; Laval U. 1173a, holotype. *5*, *6*, Top and side views of another cranidium. *7*, Pygidium; Laval U. 1173b–c, paratypes. (p. 463)
8—*Acheilus triangularis* Rasetti, n. sp. Cranidium, ×8; Laval U. 1174, holotype. (p. 463)
9–13—*Acheilus? marginatus* Rasetti, n. sp., ×5. *9*, Small cranidium; Laval U. 1175b, paratype. *10*, Libragene; Laval U. 1175c, paratype. *11*, *12*, Top and side views of cranidium; Laval U. 1175a, holotype. *13*, Pygidium; Laval U. 1175d, paratype. (p. 463)
14—*Apatokephaloides pauper* (Billings), ×4. Cranidium; Laval U. 1176, plesiotype. (p. 465)
15, *16*—*Apatokephaloides rotundatus* Rasetti, n. sp., ×3. *15*, Cranidium; U.S.N.M. 111701, paratype. *16*, Cranidium; U.S.N.M. 111700, holotype. (p. 465)
17–19—*Bayfieldia ulrichi* Rasetti, n. sp., ×4. *17*, *18*, Top and side views of cranidium; U.S.N.M. 111702, holotype. *19*, Pygidium; U.S.N.M. 111703, paratype. (p. 465)
20–22—*Bellaspidella resseri* Rasetti, n. gen. n. sp., ×6. *20*, *21*, Top and side views of cranidium; U.S.N.M. 111704, holotype. *22*, Cranidium; U.S.N.M. 111705, paratype. (p. 466)
23, *24*—*Bellaspidella minor* Rasetti, n. sp., ×6. Cranidia; Laval U. 1177a, b, holotype and paratype. (p. 466)
25–27—*Bellaspidella? latifrons* Rasetti, n. sp., ×6. *25*, *26*, Top and side views of cranidium; U.S.N.M. 111707, holotype. *27*, Cranidium; U.S.N.M. 111708, paratype. (p. 466)
28, *29*—*Bellaspis? granulata* Rasetti, n. sp., ×6. Top and side views of cranidium; Laval U. 1182a, holotype. (p. 467)
30, *31*—*Bellaspis? tuberculata* Rasetti, n. sp., ×5. Side and top views of cranidium; Laval U. 1179a, holotype. (p. 467)
32, *33*—*Bellaspis? ulrichi* Rasetti, n. sp., ×5. Side and top views of cranidium; U.S.N.M. 111718, holotype. (p. 467)
34–36—*Bellaspis billingsi* Rasetti, n. gen., n. sp. *34*, *35*, Top and side views of cranidium, ×5; Laval U. 1178a, holotype. *36*, Larger cranidium, ×3; Laval U. 1178b, paratype. (p. 467)



Rasetti, Upper Cambrian Trilobites



Rasetti, Upper Cambrian Trilobites

verge even when seen from above, as in *K. cylindrica*. In the latter species, however, the fixigenes rise almost to the level of the glabella, and the palpebral lobes are turned upward. These features are clearly seen in the front view of a cranidium of *K. cylindrica*, reproduced for this purpose (plate 61, figure 8). In *K. maior*, the glabella rises above the fixigenes, and the palpebral lobes are not elevated. These characters are also present to some extent in *Keithiella depressa*, and more definitely in the various species of *Keithia*.

The specimens are exfoliated, and the impression of the lower surface is irregularly granulated. Length of holotype cranidium 16 mm.

Lévis conglomerate, probably from North Ridge (boulder unknown). Holotype, U.S.N.M. no. 111717.

Genus LEIOCORYPHE Clark, 1924
LEIOCORYPHE TRANSVERSA
Rasetti, n. sp.
Plate 61, figure 9

This species is chiefly characterized by the great relative width of the cranidium. Cranidium strongly convex longitudinally. Anterior outline regularly rounded, except for a pair of exceedingly faint indentations that represent the facial sutures. There appear to be no palpebral lobes. Posterior outline of cranidium sinuous, the axial part and the posterolateral limbs extending backward. There is no trace of the occipital and dorsal furrows.

Surface smooth. Length of holotype cranidium 4 mm., width 6.5 mm.

Boulder 32, Guay's quarry. Holotype, Laval Univ. no. 1183.

Genus LEVISELLA Ulrich, 1930
LEVISELLA OWENI (Billings)
Plate 61, figure 11

Dikelocephalus oweni BILLINGS, 1860, Canadian Naturalist, vol. 5, p. 310, fig. 8; 1863, Geology of Canada, p. 236, fig. 259; 1865, Canada Geol. Survey, Paleozoic fossils, vol. 1, p. 402, fig. 379.
Anomocarella? oweni, WALCOTT, 1914, Smithsonian Misc. Coll., vol. 57, no. 13, p. 251.
Richardsonella oweni, RAYMOND, 1924, Boston Soc. Nat. History Proc., vol. 37, p. 439.
Levisella oweni, Ulrich, 1930, in ULRICH and

EXPLANATION OF PLATE 61

FIGS. *1, 2—Glyptometopus laflammei* (Clark). Top and side views of an exfoliated cranidium, ×5; U.S.N.M. 111728, plesiotype. (p. 467)
3–5—Keithia connexa Rasetti, n. sp., ×2. *3*, Exfoliated cranidium; U.S.N.M. 111710, paratype. *4, 5*, Top and side views of exfoliated cranidium; U.S.N.M. 111709, holotype. (p. 468)
6, 7—Keithiella maior Rasetti, n. sp., ×1.5. Top and side views of exfoliated cranidium; U.S.N.M. 111717, holotype. (p. 468)
8—Keithiella cylindrica (Billings). Front view of an exfoliated cranidium, ×3; U.S.N.M. 111730, plesiotype. (p. 469)
9—Leiocoryphe transversa Rasetti, n. sp. Cranidium, ×3; Laval U. 1183, holotype. (p. 469)
10—Levisella brevifrons Rasetti. Almost complete partly exfoliated shield, ×2; Laval U. 1184, plesiotype. (p. 470)
11—Levisella oweni (Billings). Almost complete exfoliated cephalon, ×2; U.S.N.M. 111722, plesiotype. (p. 469)
12, 13—Loganellus macropleurus Rasetti. *12*, Small exfoliated cephalon, ×5; Laval U. 1185a, plesiotype. *13*, Thorax and pygidium, ×1.5; Laval U. 1185b, plesiotype. (p. 470)
14—Platydiamesus inornatus (Raymond). Cranidium, ×3; Laval U. 1189, plesiotype. (p. 472)
15—Platydiamesus levisensis Rasetti. Exfoliated cranidium, ×1.5; U.S.N.M. 111724, plesiotype. (p. 472)
16—Parabolina? incerta Rasetti, n. sp. Exfoliated cranidium, ×3; U.S.N.M. 111720, holotype. (p. 471)
17–19—Onchonotus? sedgwicki (Billings), ×3. *17, 18*, Top and side views of exfoliated cranidium; U.S.N.M. 111726, plesiotype. *19*, Partly exfoliated cranidium; U.S.N.M. 111727, plesiotype. (p. 470)
20–22—Onchonotus sulcatus Rasetti, n. sp., ×6. *20*, Cranidium; Laval U. 1186b, paratype. *21, 22*, Side and top views of cranidium; Laval U. 1186a, holotype. (p. 470)
23–25—Paranorwoodia venusta Rasetti, n. gen. n. sp., ×6. *23*, Cranidium; Laval U. 1187b, paratype. *24, 25*, Top and side views of cephalon; Laval U. 1187a, holotype. (p. 471)
26—Punctularia brevifrons Rasetti, n. sp. Cranidium, ×8; Laval U. 1192, holotype. (p. 472)
27—Phoreotropis sp. undet. Cranidium, ×6; Laval U. 1188. (p. 471)
28, 29—Phoreotropis? marginata Rasetti, n. sp. Top and side views of cranidium, ×5; U.S.N.M. 111711, holotype. (p. 471)
30—Platydiamesus depressus Raymond. Cranidium, ×3; U.S.N.M. 111729, plesiotype. (p. 472)

RESSER, Milwaukee Public Mus. Bull., vol. 12, p. 17, footnote.

Levisella oweni, RASETTI, 1944, Jour. Paleontology, vol. 18, p. 246, pl. 38, figs. 5–7.

Among the numerous specimens in the U.S.N.M. collections is the almost complete cephalon illustrated. The photograph clearly shows the impression of the doublure of the coalescent libragenes. It appears that the doublure carried a series of puncta corresponding to the pits in the anterior furrow on the cranidium. Possibly, the walls of these pits connected the dorsal and ventral shields, thus strengthening the carapace. This structure seems to be similar to the one on the brim and epistomal plate of *Cryptolithus*.

Boulder A-4, probably from North Ridge. Plesiotype, U.S.N.M. no. 111722.

LEVISELLA BREVIFRONS Rasetti
Plate 61, figure 10

Levisella brevifrons RASETTI, 1944, Jour. Paleontology, vol. 18, no. 3, p. 246, pl. 38, figs. 10–12.

An almost complete shield was recovered after the species had been described. The thorax has 11 segments; the pleura taper toward their ends, the posterior ones curving backward and to some extent enveloping the pygidium. A remarkable feature, also present in some species of *Loganellus*, is the macropleural development of the fifth segment. Its pleura, when complete, probably reached as far back as the end of the pygidium.

Boulder 15, North Ridge. Plesiotype, Laval Univ. no. 1184.

Genus LOGANELLUS Devine, 1863

LOGANELLUS MACROPLEURUS Rasetti
Plate 61, figures 12, 13

Loganellus macropleurus RASETTI, 1944, Jour. Paleontology, vol. 18, no, 3, p. 247, pl. 38, figs. 15–17.

A small, almost complete cephalon and another specimen preserving the thorax and pygidium are figured.

It will be noticed that the thorax and pygidium closely resemble those of *Levisella brevifrons*, except for the fact that the thoracic pleura are straighter and the posterior ones do not envelop the pygidium.

As in *Levisella*, the libragenes are not separated by a median suture, and the anterior portion of the facial suture remains wholly intramarginal.

Boulder 15, North Ridge. Plesiotypes, Laval Univ. nos. 1185a-b.

Genus ONCHONOTUS Raymond, 1924

ONCHONOTUS SULCATUS Rasetti, n. sp.
Plate 61, figures 20–22

This is a small species for the genus, none of the cranidia exceeding 3 mm. in length. Glebella strongly convex, tapering, almost straight-sided, regularly rounded in front. Posterior glabellar furrows rather well impressed for a species of *Onchonotus*. Occipital segment somewhat elevated in the middle. Fixigenes rising to a low ridge all around the dorsal furrow. Brim sloping downward, with the upturned, nasute rim that is a characistic feature of several species of the genus.

Boulder 57, North Ridge. Holotype and paratype, Laval Univ. nos. 1186a-b.

ONCHONOTUS? SEDGWICKI (Billings)
Plate 61, figures 17–19

Menocephalus sedgwicki BILLINGS, 1860, Canadian Naturalist, vol. 5, p. 316, fig. 19; 1863, Geology of Canada, p. 237, fig. 266; 1865, Canada Geol. Survey, Paleozoic Fossils, vol. 1, p. 407, fig. 387.

Apatokephalus? sedgwicki, CLARK, 1924, Bull. Am. Paleontology, vol. 10, no. 41, p. 14.

"Menocephalus" sedgwicki, RASETTI, 1944, Jour. Paleontology, vol. 18, no. 3, p. 258, pl. 36, fig. 56.

The United States National Museum collections contain several cranidia of this species. Hence the writer is able to supply additional information and to attempt a generic assignment.

When fairly complete cranidia are examined, it appears that *Menocephalus sedgwicki* can be referred to *Onchonotus*. At first, the cranidium seems to bear little resemblance to the more familiar smooth forms, such as *O. nasutus* and *O. richardsoni*. The type of the genus, however, is *O. globosus*, which occupies an intermediate position between the smooth species and *O.? sedgwicki*.

The chief characters that distinguish *O.? sedgwicki* from *O. globosus* are the more elongated and less convex glabella, and the presence of well-developed glabellar furrows. The sloping brim and the upturned, nasute rim are characterisic of *Onchonotus*.

The palpebral lobes have approximately the same size and position as in *O. globosus*. The tuberculated surface is common to the two species.

The general aspect of the cranidium, and in particular the convex fixigenes forming a low ridge outside of the dorsal furrow, are suggestive of the early Ordovician genus *Hystricurus*. In *Hystricurus*, however, the anterior outline of the cranidium is regularly rounded and not pointed as in *Onchonotus*. It is possible that the two genera are closely related.

Boulders A-3 and A-4, probably from North Ridge. Plesiotypes, U.S.N.M. nos. 111726, 111727.

Genus PARABOLINA Salter, 1849

PARABOLINA? INCERTA Rasetti, n. sp.

Plate 61, figure 16

A single cranidium from Lévis cannot be referred to any North American genus, but bears a remarkable resemblance to certain genera of the Olenidae from the Atlantic province. It is assigned to *Parabolina* with extreme doubt, since most of the suggested references of American trilobites to the Olenidae proved to be mistaken.

Glabella weakly convex, subrectangular. Two pairs of oblique glabellar furrows, not continuous across the glabella, and isolated from the dorsal furrows. Fixigenes about one-third as wide as the glabella. Ocular ridges strong, directed slightly backward. Palpebral lobes not preserved, but obviously small and situated in advance of the glabellar midpoint. Brim as wide as the fixigenes, weakly convex, with a narrow elevated rim. Anterior facial sutures parallel. Occipital ring bearing a small tubercle. Length of cranidium 4 mm.

Boulder A-3, probably from North Ridge. Holotype, U.S.N.M. no. 111720.

Genus PARANORWOODIA Rasetti, n. gen.

Small proparian trilobites. Cephalon rather strongly convex as a whole, with a narrow concave border. Glabella occupying about one-half of the length and one-fourth of the width of the cephalon, convex, cylindrical, unfurrowed. Occipital furrow strongly impressed; occipital segment narrow and simple. Eyes exceedingly small, situated at the level of the anterior end of the glabella; ocular ridges faint, transverse. Libragenes very small, narrowly triangular. Anterior facial sutures slightly convergent; posterior branch reaching the margin much in advance of the genal angle. Genal spines strong, curving inward.

Genotype, *P. venusta* Rasetti, n. sp.

Remarks.—Paranorwoodia is obviously related to the early Upper Cambrian genera *Norwoodia*, *Norwoodella* and *Holcacephalus*. These four genera constitute a small, homogeneous proparian family. *Levisaspis* seems clearly to represent an early Ordovician descendant of the same group of trilobites.

PARANORWOODIA VENUSTA Rasetti, n. sp.

Plate 61, figures 23–25

The generic description and the illustrations present all the known characters of this species. The surface is smooth. Length of largest cranidium 3 mm.

Boulder 57, North Ridge. Holotype and paratypes, Laval Univ. nos. 1187a-d.

Genus PHOREOTROPIS Raymond, 1924

PHOREOTROPIS sp. undet.

Plate 61, figure 27

A single cranidium of an undoubted species of *Phoreotropis* was collected at Lévis and is figured, in order to show the presence of the genus in the Lévis conglomerate. It probably does not belong to either of Raymond's species, but the specimen is too small and imperfect to warrant description. Length of cranidium 1.5 mm.

Boulder 59, North Ridge. Laval Univ. no. 1188.

PHOREOTROPIS? MARGINATA Rasetti, n. sp.

Plate 61, figures 28, 29

This species is not quite typical of *Phoreotropis*, but seems to fit better in this genus than in any other described. Glabella almost parallel-sided, well defined by the dorsal furrows at the sides but hardly defined in front, where it merges with the convex brim. Glabellar furrows very shallow, occipital furrow well impressed. The main character that does not agree with *Phoreotropis* is the presence of a narrow, convex rim. Fixigenes half as wide as the glabella, moderately convex. Narrow, curved ocular ridges connect the glabella

with the small palpebral lobes, which are situated somewhat in advance of the glabellar midpoint. The facial sutures in front of the eyes are directed straight forward; the posterior branch defines rather wide posterolateral limbs. Surface smooth. Length of holotype cranidium 2.5 mm.

Boulder A-2, probably from North Ridge. Holotype and paratypes, U.S.N.M. nos. 111711, 111712, 111712a-c.

Genus PLATYDIAMESUS Raymond, 1937
PLATYDIAMESUS DEPRESSUS Raymond
Plate 61, figure 30

Platydiamesus depressus RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, no. 8, p. 1109, pl. 2, fig. 20.

This species, described from the Gorge, seems to be represented in the Lévis conglomerate. A cranidium assigned to *P. depressus* is figured.

Boulder A-1, probably from North Ridge. Plesiotype, U.S.N.M. no. 111729.

PLATYDIAMESUS INORNATUS (Raymond)
Plate 61, figure 14

Asaphiscus inornatus RAYMOND, 1924, Boston Soc. Nat. History Proc., vol. 37, p. 409, pl. 12, fig. 23.
Platydiamesus inornatus, RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1110, pl. 2, figs. 18–19.

Rare specimens that occur at Lévis were compared with casts of the types from the Gorge and failed to reveal any significant differences. The species differs from *P. depressus* in the less tapering glabella and the almost obsolete occipital furrow.

Boulder 32, Guay's quarry. Plesiotype, Laval Univ. no. 1189.

PLATYDIAMESUS LEVISENSIS Rasetti
Plate 61, figure 15

Platydiamesus levisensis RASETTI, 1944, Jour. Paleontology, vol. 18, no. 3, p. 251, pl. 37, fig. 40.

The United States National Museum collections contain a few cranidia of this species. One of them is figured, as the previously illustrated holotype was a poor specimen.

Boulder A-3, probably from North Ridge. Plesiotype, U.S.N.M. no. 111724.

Genus PLETHOMETOPUS Ulrich, 1930
PLETHOMETOPUS LAEVIS (Raymond)
Plate 62, figure 3

Plethopeltis laevis RAYMOND, 1924, Boston Soc. Nat. History Proc., vol. 37, p. 417, pl. 13, fig. 3.
Plethometopus laevis, ULRICH, 1930, Missouri Bur. Geology and Mines, ser. 2, vol. 24, p. 221.

This species, described from the Gorge, appears to be represented at Lévis. It is well characterized by the subtriangular shape of the cranidium, the deep occipital furrow, and the rounded occipital ring.

Boulder 14, South Ridge. Plesiotype, Laval Univ. no. 1190.

PLETHOMETOPUS OBTUSUS Rasetti, n. sp.
Plate 62, figures 1, 2

This species closely resembles the genotype, *P. armatus* (Billings), in the general shape and convexity of the cranidium. The glabella is defined at the sides by faint dorsal furrows, but not defined in front even on exfoliated specimens. The facial sutures slightly diverge in front of the palpebral lobes; the latter have the same size and position as in *P. armatus*.

The only important feature that distinguishes *P. obtusus* from Billings' species is the shape of the occipital segment, which forms a broadly subtriangular spine, instead of possessing a long, sharp spine as in *P. armatus*.

Length of largest complete cranidium 15 mm. Fragments indicate the presence of individuals of larger size.

Boulder 57, North Ridge. Holotype and paratypes, Laval Univ. nos. 1191a-c.

Genus PUNCTULARIA Raymond, 1937
PUNCTULARIA BREVIFRONS Rasetti, n. sp.
Plate 61, figure 26

This species agrees with the genotype, *P. ornata* Raymond, in all essential respects, differing mainly in the proportionately shorter and wider glabella and the narrower preglabellar area. Glabella subrectangular, with two pairs of furrows faintly impressed. Preglabellar area very narrow; rim wide, convex, somewhat arched. Palpebral lobes opposite the glabellar midpoint, somewhat elevated, distant from the glabella one-fourth of the glabellar width. Whole surface

of test covered with puncta as in *P. ornata*. Length of holotype cranidium 2.2 mm.

Raymond states that *Punctularia* has proparian sutures. The writer is unable to see any convincing evidence for this statement either on the cast of Raymond's type or on cranidia of the new species.

Boulder 39, North Ridge. Holotype, Laval Univ. no. 1192.

Genus RESSERASPIS Rasetti, n. gen.

Large trilobites chiefly characterized by the peculiar pygidium. Cranidium weakly convex as a whole; glabella large, weakly convex, tapering, unfurrowed. Palpebral lobes small, close to the glabella and opposite its midpoint. Anterior facial sutures moderately divergent. Brim rather narrow, divided into a preglabellar area and a slightly convex rim.

Pygidium less than one and one-half times as wide as long, with a regularly semicircular posterior outline and widely rounded anterior angles. Axis strongly prominent, cylindrical, bluntly terminated, with a few moderately impressed furrows. Pleural lobes with little relief; there are faint furrows impressed in the proximity of the axis, and a slightly concave, unfurrowed marginal area. A sharp ridge extends from the extremity of the axis to the posterior margin.

Genotype, *R. carinata* Rasetti, n. sp.

Remarks.—The cranidium is not unlike those of several Upper Cambrian genera. It might perhaps best be compared with *Lecanopyge*, from which it differs in the wider brim and more divergent facial sutures. The pygidium, with its post-axial ridge, has an unusual aspect.

Should the cranidium and pygidium prove to belong to different trilobites, the name should be reserved for the pygidium, since the holotype of the type species is a pygidium.

RESSERASPIS CARINATA Rasetti, n. sp.
Plate 62, figures 4, 5

There is little to add to the generic description. The specimens are mostly exfoliated, but what remains of the test shows that the upper surface is smooth, Length of largest cranidium 25 mm. Length of largest pygidium 19 mm., width 27 mm.

The two shields are assigned to one species, as they represented the only large trilobite in the boulder from which they were recovered.

Boulder 60, South Ridge. Holotype (pygidium), and paratypes, Laval Univ. nos. 1193a–d.

Genus TAENICEPHALINA Rasetti, n. gen.

Known from the cranidium alone. Glabella moderately convex, well defined by the dorsal furrows, tapering, rounded in front. Glabellar furrows faintly impressed. Fixigenes convex, about one-third as wide as the glabella. Palpebral lobes small, opposite the glabellar midpoint; ocular ridges weakly elevated. Anterior facial sutures almost parallel in front of the eyes, then curving inward and crossing the rim obliquely. Brim narrow, with a convex rim; anterior angles turned downward. Occipital furrow well impressed, occipital segment simple.

Genotype, *T. lechevalieri* Rasetti, n. sp.

Remarks.—The present genus and several others from the *Hungaia* zone are difficult to characterize, as they possess many of the generalized trilobite features and hence resemble many Cambrian genera. *Taenicephalina* somewhat resembles certain early Upper Cambrian genera, such as *Talbotina* and *Taenicephalus*, but it is doubtful that any close relationship is involved. It is possible that *Talbotina? levisensis* Rasetti should be referred to *Taenicephalina*, although the brim structure is different and the glabellar furrows are much more deeply impressed.

TAENICEPHALINA LECHEVALIERI
Rasetti, n. sp.
Plate 62, figures 6–8

Cranidium moderately convex as a whole. Glabella almost furrowless even in exfoliated specimens. Fixigenes convex; brim of moderate width, slightly convex, divided by a deep, straight anterior furrow. Rim convex, with a somewhat pointed anterior outline suggesting that the facial sutures reach the margin only at the center. Palpebral lobes very small, set off by a faint furrow. Posterolateral limbs relatively short. Surface of test smooth. Length of holotype cranidium 8 mm.

Boulder 60, South Ridge. Holotype and paratypes, Laval Univ. nos. 1194a–f.

Genus TATONASPIS Kobayashi, 1935

TATONASPIS LEVISENSIS Rasetti

Plate 62, figures 11–14

Tatonaspis levisensis RASETTI, 1944, Jour. Paleontology, vol. 18, no. 3, p. 257, pl. 37, figs. 11–12.

A good deal of new material of this species resulted from the writer's own collections, and numerous cranidia are preserved in the United States National Museum. Hence a more complete description becomes possible.

An almost perfect cephalon preserving the test, collected by the writer, is strongly suggestive of such Ordovician genera as *Nileus* and *Symphysurus*. The entire cephalon has more relief than would be expected from the cranidium alone, on account of the drooping attitude and convexity of the libragenes. The latter possess short, slender genal spines. In front view, the cephalon shows a wide, arched, transversely striated, vertical rim. The anterior portion of the facial suture cuts this striated rim so that only the top of the central part belongs to the cranidium. There is no median suture between the libragenes. The visual surface of the eye consists of a low, vertical, semicircular band; the facets cannot be distinguished. The whole surface of the cephalon, excepting the striated rim, is punctate.

On the outer surface of the test, the glabella is hardly outlined. Among exfoliated specimens, there is a good deal of variability in the distinctness of the dorsal furrows. Extreme specimens might easily be assigned to different species; but the examination of numerous individuals revealed a continuous range of variability in this character, so that there appears to be no basis for a specific distinction. The exfoliated cranidium figured has deeper dorsal furrows than the equally exfoliated syntypes.

The pygidium of this relatively common species has not been identified.

Plesiotypes, Laval Univ. nos. 1195a–c (from boulder 57, North Ridge) and U.S.N.M. no. 111723 (from boulder A-4, probably collected on North Ridge).

Genus ULRICHASPIS Rasetti, n. gen.

Large, peculiar trilobites known from the cranidium alone. Glabella weakly convex but defined by deep dorsal furrows, subtrapezoidal. Two pairs of strong, oblique glabellar furrows. Brim wide, divided into a gently convex preglabellar area and a wide, convex, strongly arched rim. Seen from the front, the rim describes an almost complete semicircle; hence the anterior angles of the cranidium are strongly turned downward. Palpebral lobes not preserved, but obviously small, situated somewhat in advance of the anterior end of the glabella. Ocular ridges strong, directed forward. Posterolateral limbs large. Occipital segment of average width. Surface of preglabellar area with irregular longitudinal striations.

Genotype, *U. paradoxa* Rasetti, n. sp.

Remarks.—The writer does not know of any described trilobite to which the present form might be compared. The exceedingly advanced position of the eyes with respect to the glabella, and the peculiar brim structure, constitute an unusual combination of characters among Cambrian trilobites.

ULRICHASPIS PARADOXA Rasetti, n. sp.

Plate 62, figures 9, 10, 15

The generic description and the illustrations supply all the available information about this species. Two fragmentary cranidia are all the material in hand. The larger cranidium is 18 mm. long and, if complete, would be about 40 mm. wide.

Lévis conglomerate (boulder unknown). Since the faunal associations of this species are unknown, its reference to the Upper Cambrian *Hungaia* zone is necessarily tentative.

Holotype and paratype, U.S.N.M. nos. 111713, 111714.

Genus WESTONASPIS Rasetti, n. gen.

Small trilobites known from the cranidium. Glabella moderately convex, tapering; dorsal furrows deeply impressed posteriorly but becoming shallower toward the front, so that the glabella is hardly set off from the brim either by a furrow or by a change in slope. Glabellar furrows short, oblique; occipital furrow deeply impressed. Brim convex, without rim; fixigenes convex, about half as wide as the glabella. Palpebral lobes small, slightly elevated, opposite the glabellar midpoint. Facial sutures presenting little change of direction behind and in front of the palpebral lobes, hence converging in front of the eyes.

Genotype, *W. laevifrons* Rasetti, n. sp.

Remarks.—The only known species of the genus does not seem to present sufficient similarity to any described trilobite to suggest possible affinities.

The genus is named in honor of T. C. Weston, who collected many new species of Lévis fossils for the Geological Survey of Canada.

WESTONASPIS LAEVIFRONS Rasetti, n. sp.
Plate 62, figures 16, 17

There remains little to be added to the generic description. Posterior glabellar furrows deeply impressed and, although short, almost isolating small basal lobes. Two other pairs of furrows are visible. Faint ocular ridges can be distinguished under proper lighting. The surface of the glabella and of the posterolateral limbs is faintly granulose. Length of holotype cranidium 2.5 mm.

Boulder 14, South Ridge. Holotype and paratype, Laval Univ. nos. 1196a–b.

Genus ZACOMPSUS Raymond, 1924
ZACOMPSUS CONVEXUS Rasetti, n. sp.
Plate 62, figure 21

Glabella clavate, straight-sided, strongly convex transversely, unfurrowed. Fixigenes and brim convex, the latter steeply inclined. There is an exceedingly narrow and low rim. Eyes small, situated almost opposite the anterior end of the glabella; ocular ridges faint, directed slightly forward. Surface smooth. Length of holotype cranidium 2.5 mm.

This species differs from the genotype, *Z. clarki* Raymond, chiefly in the structure of the brim, the more straight-sided glabella, and the much fainter ocular ridges.

Lévis conglomerate, probably from North Ridge (boulder unknown). Holotype and paratype, U.S.N.M. nos. 111715, 111716.

ZACOMPSUS? LEVISENSIS Rasetti
Plate 62, figures 18, 19

Zacompsus? levisensis RASETTI, 1944, Jour. Paleontology, vol. 18, no. 3, p. 258, pl. 39, fig. 6.

A new cranidium is figured in top and side views in order to bring out the tumid structure of the brim; this feature was not clearly visible on the illustration of the holotype.

The remarkable resemblance of this form to certain species of *Olenus* from the Atlantic province should be noticed.

Boulder 15, North Ridge. Plesiotype, Laval Univ. no. 1197a.

ZACOMPSUS? PUNCTATUS Rasetti, n. sp.
Plate 62, figure 20

Like the preceding species, the present one differs from typical *Zacompsus* in the parallel-sided glabella and the presence of glabellar furrows. Glabella long and narrow, cylindrical, rounded in front. Two pairs of glabellar furrows represented by pits in the dorsal furrows. Occipital segment somewhat expanded. Brim and palpebral lobes poorly preserved; the latter apparently occupied an extremely advanced position. Surface of glabella smooth, fixigenes punctate. Length of holotype cranidium 2.5 mm.

Boulder 32, Guay's quarry. Holotype, Laval Univ. no. 1198.

UNASSIGNED PYGIDIA

The matching of pygidia and cranidia among the trilobites of the Lévis conglomerate is a particularly difficult task. Usually the most fossiliferous boulders contain a large number of genera and species. Moreover, the occurrence of the fossils indicates that the trilobite shields, after the different parts had separated, were sorted by the currents according to size and shape, and hence the parts of the same trilobite may not lie close together in the rock.

A peculiar fact is the relatively small number of pygidia that have been recovered. Both in the United States National Museum collections and in the writer's own, the cranidia outnumber the pygidia in the ratio of about ten to one. The cranidia of certain genera, such as *Onchonotus*, *Stenopilus* and *Tatonaspis*, are common in some of the boulders; yet no corresponding pygidia were recovered from the same rock.

The writer believes that it is worth while to describe and figure a few of the unassigned pygidia, *i.e.*, those which present such characteristic features as to make their identification easy. It is hoped that other students of Cambrian faunas may be able to identify similar pygidia from other localities and to assign them to their respective genera. For a few of the described pygidia, tentative assignments are suggested.

UNASSIGNED PYGIDIUM NO. 1
Plate 62, figure 22

This pygidium has a subtriangular shape and considerable relief. Axis narrow, prominent, cylindrical, with seven or eight segments visible. Pleural lobes steeply inclined, with a concave border. About six pairs of furrows and grooves extend to the posterior margin.

Raymond assigned a similar pygidium from the Gorge to *Highgatea bisinuata* (=*Loganellus*), to which it almost certainly does not belong. Association with the cranidia at both localities suggests the possibility that these pygidia belong to species of *Keithiella*.

The figured specimen is from boulder 32, Guay's quarry. Laval Univ. no. 1199.

UNASSIGNED PYGIDIUM NO. 2
Plate 62, figure 23

Pygidium somewhat less than twice as wide as long, depressed. Axis less than half the length of the pygidium, tapering, poorly defined, almost unfurrowed. Pleural lobes depressed, slightly concave, unfurrowed except for the anterior marginal furrow. Anterior angles truncated at an angle of 30° for a considerable distance. Posterior outline perfectly semicircular. Length of largest pygidium 9 mm., width 14 mm.

Although this pygidium is not rare in boulder 32, Guay's quarry, the writer has been unable to assign it to any of the associated cranidia.

Laval Univ. nos. 1200a–d.

UNASSIGNED PYGIDIUM NO. 3
Plate 62, figure 31

Pygidium somewhat less than twice as wide as long, depressed. Axis slightly more than half the length of the pygidium, moderately prominent, with three faint furrows. Pleural lobes faintly furrowed in the proxim-

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EXPLANATION OF PLATE 62

FIGS. *1, 2—Plethometopus obtusus* Rasetti, n. sp. *1*, Exfoliated cranidium, ×1.5; Laval U. 1191a, holotype. *2*, Smaller cranidium preserving most of the test, ×3; Laval U. 1191b, paratype. (p. 472)

3—Plethometopus laevis (Raymond). Cranidium, ×3; Laval U. 1190, plesiotype. (p. 472)

4, 5—Resseraspis carinata Rasetti, n. gen. n. sp., ×1.5. *4*, Cranidium lacking most of the test; Laval U. 1193b, paratype. *5*, Exfoliated pygidium; Laval U. 1193a, holotype. (p. 473)

6–8—Taenicephalina lechevalieri Rasetti, n. gen., n. sp., ×2. *6*, Cranidium lacking the test; Laval U. 1194b, paratype. *7, 8*, Top and side views of cranidium; Laval U. 1194a, holotype. (p. 473)

9, 10, 15—Ulrichaspis paradoxa Rasetti, n. gen., n. sp., ×1.5. *9*, Small exfoliated cranidium; U.S.N.M. 111714, paratype. *10, 15*, Top and side views of larger exfoliated cranidium; U.S.N.M. 111713, holotype. (p. 474)

11–14—Tatonaspis levisensis Rasetti. *11–13*, Top, side and front views of almost perfect cephalon, ×4; Laval U. 1195a, plesiotype. *14*, Exfoliated cranidium with well-impressed dorsal furrows, ×2; U.S.N.M. 111723, plesiotype. (p. 474)

16, 17—Westonaspis laevifrons Rasetti, n. gen., n. sp., ×6. Side and top views of cranidium; Laval U. 1196a, holotype. (p. 475)

18, 19—Zacompsus? levisensis Rasetti. Top and side views of cranidium, ×5; Laval U. 1197a, plesiotype. (p. 475)

20—Zacompsus? punctatus Rasetti, n. sp. Cranidium, ×6; Laval U. 1198, holotype. (p. 475)

21—Zacompsus convexus Rasetti, n. sp. Cranidium, ×5; U.S.N.M. 111715, holotype. (p. 475)

22—Unassigned pygidium no. 1. Exfoliated specimen, ×2; Laval U. 1199. (p. 476)

23—Unassigned pygidium no. 2, ×2; Laval U. 1200a. (p. 476)

24, 25—Unassigned pygidium no. 4. Top and side views of exfoliated specimen, ×1; Laval U. 1202a. (p. 477)

26, 27—Unassigned pygidium no. 8. Top and side views of specimen, ×5; Laval U. 1206. (p. 477)

28—Unassigned pygidium no. 11, ×6; U.S.N.M. 111721. (p. 478)

29, 30—Unassigned pygidium no. 7. Top and side views of exfoliated specimen, ×2; Laval U. 1205. (p. 477)

31—Unassigned pygidium no. 3, ×3; Laval U. 1201. (p. 473)

32, 33—Unassigned pygidium no. 9, ×5; Laval U. 1207. (p. 478)

34—Unassigned pygidium no. 6, ×5; Laval U. 1204. (p. 477)

35—Unassigned pygidium no. 5, ×4; Laval U. 1203. (p. 477)

36, 37—Unassigned pygidium no. 10, ×5; Laval U. 1207a. (p. 478)

Rasetti, Upper Cambrian Trilobites

ity of the axis; anterior marginal furrow well impressed. Anterior angles truncated at about 45° for half the distance from the axis; posterior outline semicircular. Length of pygidium 3.5 mm., width 6 mm.

Among the cranidia recovered from the same boulder, *Platydiamesus levisensis* is the only one to which this pygidium could be plausibly assigned.

Boulder 39, North Ridge. Laval Univ. no. 1201.

Unassigned pygidium no. 4
Plate 62, figures 24, 25

Pygidium large, with a poorly defined, tapering axis occupying less than half the length. No furrows either on the axial or on the pleural lobes, excepting the anterior marginal furrow. Pleural lobes fairly convex in the proximity of the axis, but slightly concave along the posterior margin. Anterior outline truncated for a considerable distance. Surface smooth. Length of largest pygidium 14 mm., width 20 mm.

This pygidium resembles those of some species of *Lecanopyge*, but the pleural lobes have more relief. All the cranidia recovered from the same boulder belong to small species, hence no assignment can be attempted.

Boulder 32, Guay's quarry. Laval Univ. nos. 1202a–b.

Unassigned pygidium no. 5
Plate 62, figure 35

Axis strongly convex, tapering, occupying one-third of the width and almost the whole length of the pygidium. Pleural lobes entirely convex, with a narrow rim. The posterior margin, when seen from the back, appears somewhat elevated at the center. Four pairs of distinct but very narrow furrows are impressed both on the axis and the pleural lobes. Pleural grooves indistinct. Length of pygidium 2.8 mm., width 4.5 mm. Surface almost smooth.

Association in the boulders suggests the possibility that this pygidium belongs to *Bienvillia corax* (Billings).

Boulder 59, North Ridge. Laval Univ. no. 1203.

Unassigned pygidium no. 6
Plate 62, figure 34

Pygidium small, with a large axis occupying half the width and almost reaching the posterior margin. Axis well defined, depressed, of almost even width; a short postaxial ridge reaches the posterior margin. Pleural lobes depressed, slightly concave; posterior outline semicircular, except for a slight notch at the center. Axis with two faint furrows; pleural lobes more distinctly furrowed than the axis, with two pairs of furrows and grooves. Surface of axis with distinct pits, of pleural lobes smooth. Length of pygidium 2.4 mm., width 4.4 mm.

Only one specimen of this peculiar pygidium was recovered, and the writer is unable to suggest a plausible assignment.

Boulder 57, North Ridge. Laval Univ. no. 1204.

Unassigned pygidium no. 7
Plate 62, figures 29, 30

Pygidium of fairly large size, strongly convex. Axis strongly convex, tapering, poorly defined posteriorly; one axial furrow besides the articulating furrow. Pleural lobes steeply inclined, convex except for a narrow marginal area at the sides. No distinct pleural furrows, except the anterior marginal furrow.

The available specimens are exfoliated, and show faint, transverse, wavy lines on the pleural lobes. Length of largest pygidium 10 mm., width 15 mm.

Association suggests the possibility that this pygidium belongs to a species of *Plethometopus*.

Boulder 38, North Ridge. Laval Univ. nos. 1205a–c.

Unassigned pygidium no. 8[1]
Plate 62, figures 26, 27

This and the next two pygidia to be described have several features in common: the large axis, strong convexity, and very oblique anterior outline of the pleural lobes. It is likely that they belong to the same genus.

Axis strongly convex, occupying most of the area of the pygidium, almost reaching the posterior margin. Pleural lobes moderately convex, with a very oblique anterior outline. No axial or pleural furrows, excepting the articulating furrow. Posterior mar-

[1] Additional material, collected after this paper was written, indicates that this pygidium belongs to *Stenopilus dubius* Rasetti.

gin with a striated doublure visible from above; remaining surface of pygidium smooth. Length of pygidium 3.8 mm., width 4.6 mm.

Boulder 32, Guay's quarry. Laval Univ. no. 1206.

Unassigned pygidium no. 9
Plate 62, figures 32, 33

Axis strongly convex, tapering, occupying about five-sixths of the pygidial length, with a distinct furrow besides the articulating furrow. Pleural lobes narrower than the axis, steeply inclined, with one furrow and one groove fairly well impressed. Posterior outline regularly rounded; anterior margin obliquely truncated and presenting a vertical, striated facet. Length of pygidium 2.8 mm., width 3.4 mm. Surface very finely granulated.

Boulder 39, North Ridge. Laval Univ. nos. 1207a–c.

Unassigned pygidium no. 10
Plate 62, figures 36, 37

This pygidium differs from the preceding chiefly in the lesser development of the furrows. Axis occupying about four-fifths of the length, poorly defined at the rear. Pleural lobes somewhat concave near the margin. Furrows absent from both the axis and the pleural lobes, excepting the anterior marginal furrow. Surface smooth. Length of pygidium 2.6 mm., width 3.2 mm.

Manuscript received September 11, 1944

This pygidium was fairly common in boulder 14, South Ridge; yet no cranidium was found to which the pygidium could be plausibly assigned.

Laval Univ. nos. 1207a–f.

Unassigned pygidium no. 11
Plate 62, figure 28

A small, rare pygidium is described because of its peculiar structure. Axis wide, almost reaching the posterior margin; consisting of the articulating ring, a prominent segment, and a fused, depressed terminal section. Pleural lobes mostly consisting of a convex rim, which merges with the axis at the center. Surface of rim and of terminal section of axis transversely striated. Length of pygidium 1.7 mm., width 2.4 mm.

The figured specimen (U.S.N.M. no. 111721) is from an unknown boulder. The same pygidium was also found in boulder 57, North Ridge.

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NEW SPECIES OF BRACHIOPODS FROM THE DEVONIAN OF ILLINOIS AND MISSOURI

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ABSTRACT.—Thirteen new species of Middle Devonian brachiopods from Illinois and Missouri, distributed among nine genera, are described as follows: *Chonetes*, four; *Camarotoechia*, two; *Hypothyridina*, one; *Stenoscisma*, two; *Athyris*, one; *Brachyspirifer*, one; *Tylothyris*, one; and *Centronella*, one. An unusual specimen of *Paraspirifer acuminatus* (Conrad) is also discussed.

THE SPECIES described and figured below are important to an understanding of the stratigraphy and correlation of the Devonian of Illinois and surrounding states. They and their importance are mentioned in a forthcoming publication on correlation of the Devonian of Illinois with that of surrounding states by G. A. Cooper and A. S. Warthin. The specimens were collected over a period of years by the writer and several colleagues. The unusual specimens of *Hypothyridina* from Missouri were collected by Dr. Josiah Bridge and the writer in 1939. The fine specimens of *Anathyris* from Missouri, the first of the genus to be found on this continent, were collected by Dr. F. E. Turner, Texas A. & M. College. The specimens from southwestern Illinois were found in part in 1936 by Dr. Preston E. Cloud and the writer and in part by Dr. A. Scott Warthin and the writer in 1942.

Acknowledgments and thanks are herewith extended to Dr. Harold Scott, University of Illinois, for the loan of specimens collected by Dr. T. E. Savage at the Devils Backbone and Bakeoven and now in the collections of the University of Illinois.

CHONETES TUMIDELLUS Cooper, n. sp.
Plate 63, figures 31, 39–43

Shell small, slightly wider than long; hinge narrower than the greatest shell width, which is near the middle. Lateral margins gently rounded; anterior margin fairly strongly rounded. Surface multicostellate, with three rounded, subdued costellae occupying a space of 1 millimeter.

Ventral valve strongly convex in lateral profile with the greatest convexity located in the posterior half; anterior profile strongly arched and with nearly straight, steeply sloping sides. Beak small; umbonal region broadly swollen, somewhat flattened in profile; median portion strongly swollen, the swelling extending nearly to the anterior margin; anterior slope steep; lateral slopes to the cardinal extremities very steep and slightly concave in profile. Three moderately long, oblique spines on the posterior margin on each side of the beak.

Dorsal valve, as in most chonetids, fairly well molded to the shape of the ventral valve; deeply concave, with the greatest concavity in the median region; lateral extremities flattened. Interarea short and twisted into an orthocline position.

Ventral interior as usual in the genus; dorsal interior with low, thick lateral plates, a short shaft, and narrowly trilobate myophore.

Measurements in mm.: holotype, length 10, midwidth 11.7, hinge width 8.8 ?, thickness at middle 2.4, height 5. Paratype (U.S.N.M. 111662), length 10.3, midwidth 11.4, hinge width 8.5, height 4?.

Holotype, U.S.N.M. 111660; paratypes, U.S.N.M. 111662, a–i.

Horizon and locality.—St. Laurent limestone (*Microcyclus* zone), along small creek, one-half mile east of Union School, south of Seventy-six, sec. 29, T. 35 N., R. 13 E., Altenburg quadrangle, Perry County, Missouri; also east slope of north end of Devils Backbone and Devils Bakeoven, 1 mile north of Grand Tower; several other localities in Union County, Illinois.

Remarks.—This species, like *C. scitulites* is related to the *C. scitulus* tribe but differs from both in having a more quadrate outline, more strongly tumid ventral valve with

a broad and swollen umbo and a very deeply concave dorsal valve. The proportions are somewhat like those of *C. yandellanus* Hall but *C. tumidellus* is larger and more tumid than the Ohio Falls species.

CHONETES SCITULITES Cooper, n. sp.
Plate 63, figures 35–38

Shell small, having the appearance of *C. scitulus*. Width about 1¼ times the length; hinge narrower than the greatest shell width; cardinal extremities obtuse; lateral margins gently convex; anterior margin broadly convex; anterior commissure slightly sulcate. Surface costellate; generally four costellae in the space of 1 millimeter.

Fairly strongly convex in lateral profile with the maximum convexity located in the posterior half; anterior profile unequally convex with the median portion inflated and with steep slopes that flatten toward the lateral margins. Umbonal region narrowly inflated and expanding anteriorly into a strongly swollen median area having a fairly steep anterior slope. Lateral slopes steep and concave in profile. Beak incurved. Posterior margin with two or three short, oblique spines on each side of the beak.

Dorsal valve deeply concave in the median area and in the umbonal region. Concavity lessening in the anterolateral areas and becoming quite shallow to flattened in the posterolateral areas and cardinal extremities.

Interiors usual for the genus; median ridge of ventral valve extending nearly to middle; lateral plates of dorsal interior low; cardinal process with short shaft.

Measurements in mm.: holotype, 7.8, midwidth 10.2, hinge width 8.3, thickness at middle 1.5, height 3.1.

Holotype, U.S.N.M. 111658; paratype, U.S.N.M. 111658a.

Horizon and locality.—Base of St. Laurent limestone, Devils Bakeoven, about 1 mile north of Grand Tower, Illinois.

Remarks.—The name given to this species is designed to indicate its relationship and general resemblance to the tribe of *C. scitulus*. The latter is not a well-understood species, but the New York and Ontario forms usually identified as *C. scitulus* differ from the Illinois species in not having the strongly swollen median area and the prominent narrowed umbo which extends a short distance posterior to the posterior margin. The Illinois species is also somewhat less strongly costellate than the New York and Ontario forms referred to *C. scitulus*.

CHONETES MEDIOLATUS Cooper, n. sp.
Plate 63, figures 32–34

Fairly large for the genus, transversely subquadrangular in outline, width about 1.5 times the length; cardinal extremities acute to nearly rectangular; sides usually sloping more or less strongly toward the middle and gently convex. Anterior margin broadly rounded. Surface costellate; costellae coarse and subangular in umbonal region; coarse costellae nearly all bifurcate at 5–6 mm. anterior to the beak where the costellae become finer. Main anterior half of shell finely costellate with 14–16 low, often indistinct costellae occupying 5 mm. at the front margin.

Lateral profile of ventral valve of low but even convexity; anterior profile broadly convex and with gentle lateral slopes. Median and posterolateral areas gently swollen, but cardinal extremities flattened; posterolateral slopes to cardinal angles gentle and slightly concave. Posterior margin marked by six short, oblique spines on each side of the beak.

Dorsal valve very slightly concave with the greatest concavity anterior to the middle. Posterolateral areas and umbonal region nearly flat. Cardinal extremities slightly concave.

Ventral interior with low median ridge reaching to about the middle; muscle marks not deeply impressed. Dorsal interior with low median ridge not reaching the middle; shaft of cardinal process short; myophore small; brachial ridges low and short.

Measurements in mm.: holotype (ventral valve), length 13.9, midwidth 20.6, hinge width 21.5, thickness 1.5; paratype (ventral valve U.S.N.M. 111652c), length 13.7, width 20.6, hinge width 22.0, thickness 2.0; paratype (dorsal valve U.S.N.M. 111652b), length 15.3, width 22.8, hinge width 22.0?.

Holotype, U.S.N.M. 111651; paratypes, U.S.N.M. 111652, a–f.

Horizon and locality.—St. Laurent limestone (81 feet above base), St. Laurent Creek, 3 miles south of St. Marys, Perry County, Missouri.

Remarks.—The size and form of this species relate it to the *C. coronatus* tribe and to the flatter species of that tribe, such as *C. amplus*, n. sp. and *C. syrtalis* (Conrad). It differs from both of these species by its smaller size, less prominent umbonal region, the prominent concentration of coarser costellae on the ventral umbo, and the generally flatter valves. This species is abundant in a bed about 81 feet above the base of the basal sandstone on St. Laurent Creek.

CHONETES AMPLUS Cooper, n. sp.
Plate 63, figures 44–46

Shell large for the genus and having the configuration of a flattened *C. coronatus;* width not quite 1.5 times the length; hinge wide but not forming the greatest shell width in old specimens; cardinal extremities with small alae in the young but with obtuse extremities in fully grown individuals; lateral margins varying from nearly straight to moderately convex; anterolateral extremities broadly rounded, and anterior margin slightly convex. Surface costellate, costellae narrowly rounded, increasing in size anteriorly and at the front of an adult generally wider than the interspaces. Costellae numbering about 10 in 5 mm. at the front of a large specimen but more numerous in younger specimens (12 in 5 mm. at the front of a specimen 18 mm. long).

Ventral valve gently convex in lateral profile and with the convexity fairly even throughout; anterior profile very broadly convex and of about the same order of convexity as the lateral profile. Umbonal region somewhat narrowly swollen, the swelling extending anteriorly and laterally to form a moderately inflated median area. Posterolateral areas flattened and with concave but gentle slopes extending to the cardinal angles. Posterior margin marked by seven or eight short, oblique spines on each side of the beak.

Dorsal valve gently concave with the maximum concavity in the median region and becoming shallower anteriorly.

Interior unknown.

Measurements in mm.: holotype a medium-sized ventral valve preserving some spines, length 17.6, width 24.6; hinge width 24.9; thickness ca. 3; paratype (larger ventral valve) length 18.7, width 28.3, thickness ca. 3; paratype (large dorsal valve U.S.N.M. 111663a), length 20.6, width 32.2, hinge width 25.5?, concavity at middle 2.

Holotype, U.S.N.M. 111656; paratypes, U.S.N.M. 111663,a–c; 111657, a.

Horizon and locality.—St. Laurent limestone (277 feet from base of basal sandstone), on St. Laurent Creek, 3 miles south of St. Marys, Perry County, Missouri.

Remarks.—It has been common practice to refer nearly all of the large chonetids in the Middle Devonian of the Midwest to the broadly conceived species *C. coronatus.* The fact is, that when these shells are studied in some detail a number of neglected species can be revived and a still greater number of new names is needed. *Chonetes amplus* differs from the shells usually referred to as *C. coronatus* in having a narrower beak, a less inflated umbonal and median region, and a generally flatter shell. *Chonetes syrtalis* from the Chenango sandstone member of the Skaneateles formation of the New York Hamilton group was hitherto placed in the synonymy of *C. coronatus.* It seems to be a quite good species and is fairly closely related to *C. amplus.* It differs however in being a larger and flatter shell than the Missouri species.

CAMAROTOECHIA MISSOURIENSIS
Cooper, n. sp.
Plate 63, figures 8–12

Shell of about usual size for the genus, subpentagonal in outline; length and width nearly equal; greatest width located about two-thirds the length from the beak. Posterolateral margins nearly straight, forming an apical angle of slightly more than 100°. Anterolateral extremities moderately rounded; anterior margin slightly convex. Surface costate, with 10–12 costae on the flanks (a possible two more indistinct and very fine) and five to seven in the sulcus, six to eight on the fold.

Ventral valve fairly evenly and gently convex in lateral profile, very gently convex in anterior profile. Tongue moderately long but not sharply geniculated; extremity of tongue narrowly rounded. Flanks bounding culcus not strongly elevated above sulcus, gently convex and with short, moderately steep slopes. Sulcus originating slightly posterior to middle of valve, shallow and gently

concave in anterior profile. Umbo moderately swollen; beak strongly incurved and slightly overhanging dorsal umbo.

Dorsal valve gently convex in lateral profile with the greatest convexity in the umbonal region. Anterior profile strongly convex, with lateral margins steep to nearly vertical. Fold originating slightly posterior to the middle, low and gently rounded in anterior profile. Flanks narrow, moderately swollen, and with steep sides. Umbonal region moderately inflated.

Dental plates short; median septum of dorsal valve not quite reaching the middle.

Measurements in mm.: holotype, length 14.7, width 14.2, thickness 9.5, width of fold 7.3, length of dorsal valve 13.3. Paratype (U.S.N.M. 111669), length 13.5, width 13.3, thickness 9.5, width of fold 7.4, length of dorsal valve 12.4.

Holotype, U.S.N.M. 111668; paratypes, 111669, a; unfigured paratypes, U.S.N.M. 111681.

Horizon and locality.—St. Laurent limestone (about 257 feet above base of basal sandstone), St. Laurent Creek, 3 miles south of St. Marys, Perry County, Missouri.

Remarks.—In its rotund form and rounded anterior this species resembles *Camarotoechia congregata* (Conrad) as identified in the New York Hamilton. It also resembles *C. horsfordi* (Hall) in the numerous ribs occupying the fold and sulcus. It differs from *C. horsfordi* however in having a well-rounded anterior margin, a much more tapering posterior, more incurved beak and much more swollen umbo. *C. missouriensis* differs from *C. congregata* in having more numerous costae in the sulcus and on the fold, in being a smaller species, and in tapering more narrowly posteriorly. In most of these respects is also differs from *C. carica* (Hall), which is related to *C. congregata*.

Camarotoechia compacta Cooper, n. sp.
Plate 63, figures 6, 7

Shell of medium size for the genus, somewhat variable, subpentagonal in outline, length and width about equal. Greatest width located at or near the middle. Posterolateral extremities nearly straight and forming an apical angle of 95°. Lateral extremities narrowly rounded; anterior margin gently convex. Surface costate, with seven or eight costae occupying the flanks, four to six costae occupying the sulcus and five to seven costae forming the fold.

Ventral valve moderately and evenly convex in lateral profile but gently and broadly convex in anterior profile. Sulcus shallow, originating at about the middle; tongue short and bluntly rounded. Umbonal and median region slightly swollen. Flanks narrow, convex, and with steep lateral slopes. Beak low and incurved over the dorsal umbo.

Dorsal valve slightly less convex than the ventral one in lateral profile but strongly arched in anterior profile. Fold originating at the middle, only slightly elevated above the flanks, gently convex in profile. Flanks gently rounded but with steep slopes to the margins. Umbonal region moderately swollen.

Ventral interior with short dental plates; dorsal interior with median septum not quite reaching the middle.

Measurements in mm.: holotype, length 10.8, width 10.6, length of dorsal valve 9.7, thickness 7; paratype (U.S.N.M. 111669a), length 11.4, width 11.3, length of dorsal valve 10.5, thickness 7.2 plus.

Holotype, U.S.N.M. 111664; paratypes, U.S.N.M. 111665, a, b.

Horizon and locality.—St. Laurent limestone (97 feet above base of basal sandstone), St. Laurent Creek, 3 miles south of St. Marys, Perry County, Missouri.

Remarks.—This is a small species that has some resemblance to *C. prolifica* (Hall) of the New York Hamilton but differs therefrom in possessing more costae in the fold and sulcus and in having a generally smaller size. It differs from *C. missouriensis*, n. sp. which occurs at a much higher level, in its smaller size, somewhat more rounded outline, and a lesser number of costae on the flanks.

Hypothyridina parva Cooper, n. sp.
Plate 63, figures 24–30

Small for the genus, pentagonal in outline, with length and width about equal. Beak obtuse, forming an angle of about 103°. Posterolateral margins nearly straight; lateral margins narrowly rounded, giving the

shell a distinct shouldered appearance; anterior margin gently convex. Surface marked by about 16 low, rounded costae with narrow interspaces. Five or six costae occupy the fold and five may be counted on the flanks.

Ventral valve strongly convex in lateral profile, somewhat narrowly humped medially in anterior profile. Median region swollen. Descent to posterolateral extremities moderately steep. Anterolateral extremities reflected and separated from the shell body by narrow grooves. Tongue truncated, long and convex in profile, the convexity extending posteriorly to the beak as a strong, rounded fold. Interior with short divergent dental plates.

Dorsal valve unevenly convex in lateral profile with the greatest convexity located just posterior to the middle and the anterior half nearly flat. Anterior profile strongly and narrowly convex, with nearly vertical sides. Umbonal region gently convex. Fold originating about 4 mm. anterior to the beak; place of fold origin narrowly convex; fold broad and flattened, occupying nearly the entire width. Flanks moderately convex, nearly vertical. Interior without a median septum.

Measurements in mm.: holotype, length 9, width 8.8, thickness 7.0; paratype (U.S.N.M. 108214h), length 8.8, width 9.6, thickness 6.3.

Holotype, U.S.N.M. 108214a; paratypes, U.S.N.M. 108214b–h.

Horizon and locality.—Callaway limestone, 2¼ miles south of Clifton City, Missouri.

Remarks.—This species is unlike any other unquestioned small member of the genus *Hypothyridina* at present described from this continent. It differs from *H.? globularis* Kindle by its much larger size, pentagonal outline, strong fold and ornamentation. *Hypothyris gregeri* Branson, which occurs in the Callaway, is a member of the genus *Stenoscisma* and is therefore not directly comparable to the species under discussion.

STENOSCISMA SAVAGEI Cooper, n. sp.
Plate 63, figures 1–5

Shell of about medium size for the genus, subelliptical in outline, with the length equal to somewhat more than two-thirds the width. Posterolateral margins gently concave; anterolateral margins narrowly rounded and anterior margin nearly straight. Beak forming an angle of about 110°. Posterior half nearly smooth; anterior half costate, four costae occupying the flanks, four in the sulcus and five on the fold.

Ventral valve gently convex in lateral profile and with the greatest convexity in the posterior half. Anterior profile very slightly convex. Region slightly posterior to the middle gently swollen. Sulcus shallow, originating a short distance anterior to the middle. Tongue short and wide. Costae bounding sulcus not much elevated above flanks. Flanks flattened, with gentle lateral slopes. Beak ridges not prominent; beak moderately incurved.

Dorsal valve gently convex in lateral profile; broadly but moderately strongly convex in anterior profile. Umbonal region moderately inflated. Fold low, flattened in anterior profile, broad, occupying more than half the width, its sides not steep or strongly elevated. Flanks gently convex; anterolateral slopes abrupt.

Septa of both valves not quite reaching the middle.

Measurements in mm.: length 11.1, width 13.4, thickness 8.4.

Holotype, University of Illinois D2727; Plastoholotype, U.S.N.M. 111655.

Horizon and locality.—Limestone between crystalline Grand Tower limestone and base of St. Laurent limestone, Devils Backbone, north of Grand Tower, Illinois.

Remarks.—Few comparable species of *Stenoscisma* have been described although the genus is well represented in the Middle Devonian of Michigan. Several species are known from the Cedar Valley limestone of Iowa and from the younger Shellrock limestone of the same state. These species, however, are at such a higher level from those under consideration that relationships between them, other than generic identity, are remote. *Stenoscisma rhomboidalis* (Hall and Clarke) and *S. gainesi* (Nettelroth) are related but smaller and much more acutely triangular species. *Stenoscisma savagei*, n. sp. differs from *S. illinoisensis*, n. sp. in its greater width, more obtuse beak and somewhat stronger and more numerous costae.

STENOSCISMA ILLINOISENSIS Cooper, n. sp.
Plate 63, figures 13–17

Shell of about medium size for the genus, subpentagonal in outline with the width very slightly greater than the length. Posterolateral margins slightly concave; anterolateral margins narrowly rounded. Anterior margin gently convex. Beak forming approximately a right angle. Posterior half nearly smooth; anterior half costate, three costae occupying the flanks, four occupying the fold and three the sulcus.

Ventral valve gently convex with the most convex portion in the umbonal region. Median region posterior to the sulcus gently convex. Sulcus shallow, occupying about half the valve width. Tongue short, truncated, strongly geniculated and flattened. Flanks flattened, occupied by three rounded costae, the inner one of which bounds the sulcus and is considerably more carinate and elevated above the others. Beak ridges prominent, fairly long; beak moderately strongly incurved.

Dorsal valve gently but unevenly convex in lateral profile, very gently convex in anterior profile and with the sides truncated. Umbonal and median regions very gently convex; lateral slopes steep and abrupt. Fold originating slightly anterior to the middle, very slightly elevated above the flanks. Lateral costae of the fold strong, broad and low; inner two costae smaller and slightly depressed below the outer ones. Flanks narrowly rounded.

Interior known only from the sutures of the septa and spondylia shown on the exterior through the shell. Ventral median septum extending anterior to the middle;

EXPLANATION OF PLATE 63

FIGS. *1–5—Stenoscisma savagei* Cooper, n. sp. Respectively dorsal, anterior, side, posterior and ventral views of the holotype (Univ. Illinois D2727), ×1, limestone between crystalline Grand Tower and St. Laurent limestones, Devils Backbone, north of Grand Tower, Illinois. (p. 483)

6–7—Camarotoechia compacta Cooper, n. sp. Posterior and dorsal views of the holotype (U.S. N.M. 111664), ×1. St. Laurent limestone (97 feet above base of basal sandstone), St. Laurent Creek, 3 miles south of St. Marys, Missouri. (p. 482)

8–12—Camarotoechia missouriensis Cooper, n. sp. Respectively dorsal, side, ventral, anterior and posterior views of the holotype (U.S.N.M. 111668), ×1. St. Laurent limestone (about 257 feet above base of basal sandstone, at same locality as preceding. (p. 481)

13–17—Stenoscisma illinoisensis Cooper, n. sp. Respectively ventral, posterior, anterior, dorsal and side views of the holotype (Univ. Illinois D505), ×1. Limestone between crystalline Grand Tower and St. Laurent limestones, Devils Backbone, north of Grand Tower, Illinois. (p. 484)

18–23—Centronella nana Cooper, n. sp. *18–19, 21, 23,* Respectively ventral, side, anterior, posterior and dorsal views of the holotype, (U.S.N.M. 111674), ×2. *20,* Holotype, dorsal view, ×1. Grand Tower limestone (base), branch of Darty Creek, about 4 miles northwest of Jonesboro, Illinois. (p. 488)

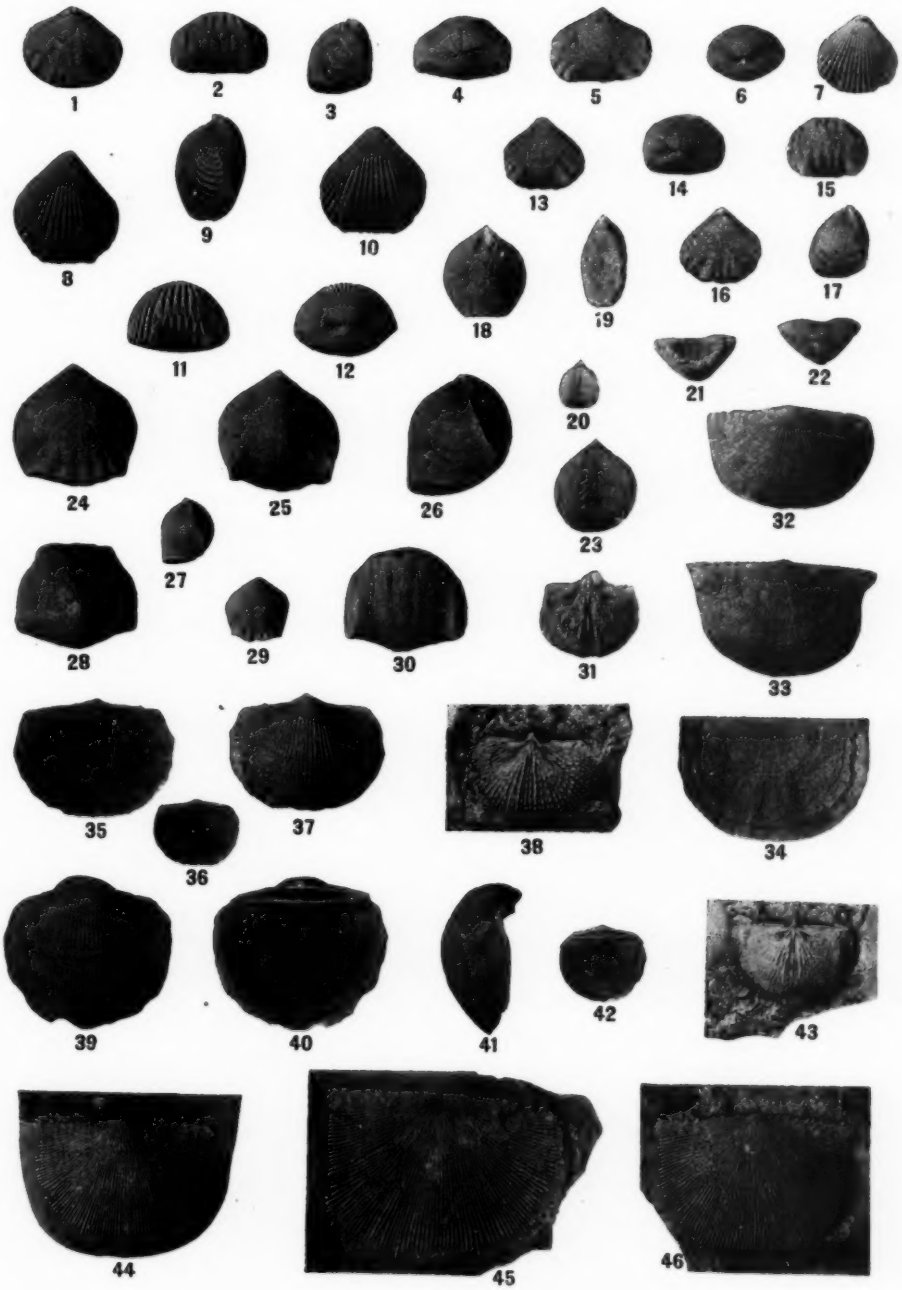
24–30—Hypothyridina parva Cooper, n. sp. *27, 29,* Respectively side and dorsal visws of the holotype (U.S.N.M. 108214a), ×1. *24–26, 28, 30,* Respectively dorsal, ventral, side, posterior and anterior views of the holotype, ×2. Callaway limestone, 2¼ miles south of Clifton, City, Missouri. (p. 482)

31, 39–43—Chonetes tumidellus Cooper, n. sp. *42,* Dorsal view of the holotype (U.S.N.M. 111660), ×1. *39–41,* Respectively ventral, dorsal and side views of the holotype, ×2. *31, 43,* Interior views of two dorsal valves, ×2, paratypes (respectively U.S.N.M. 111662a, d). St. Laurent limestone (*Microcyclus* zone), one-half mile east of Union School, Altenburg quadrangle, Missouri. (p. 479)

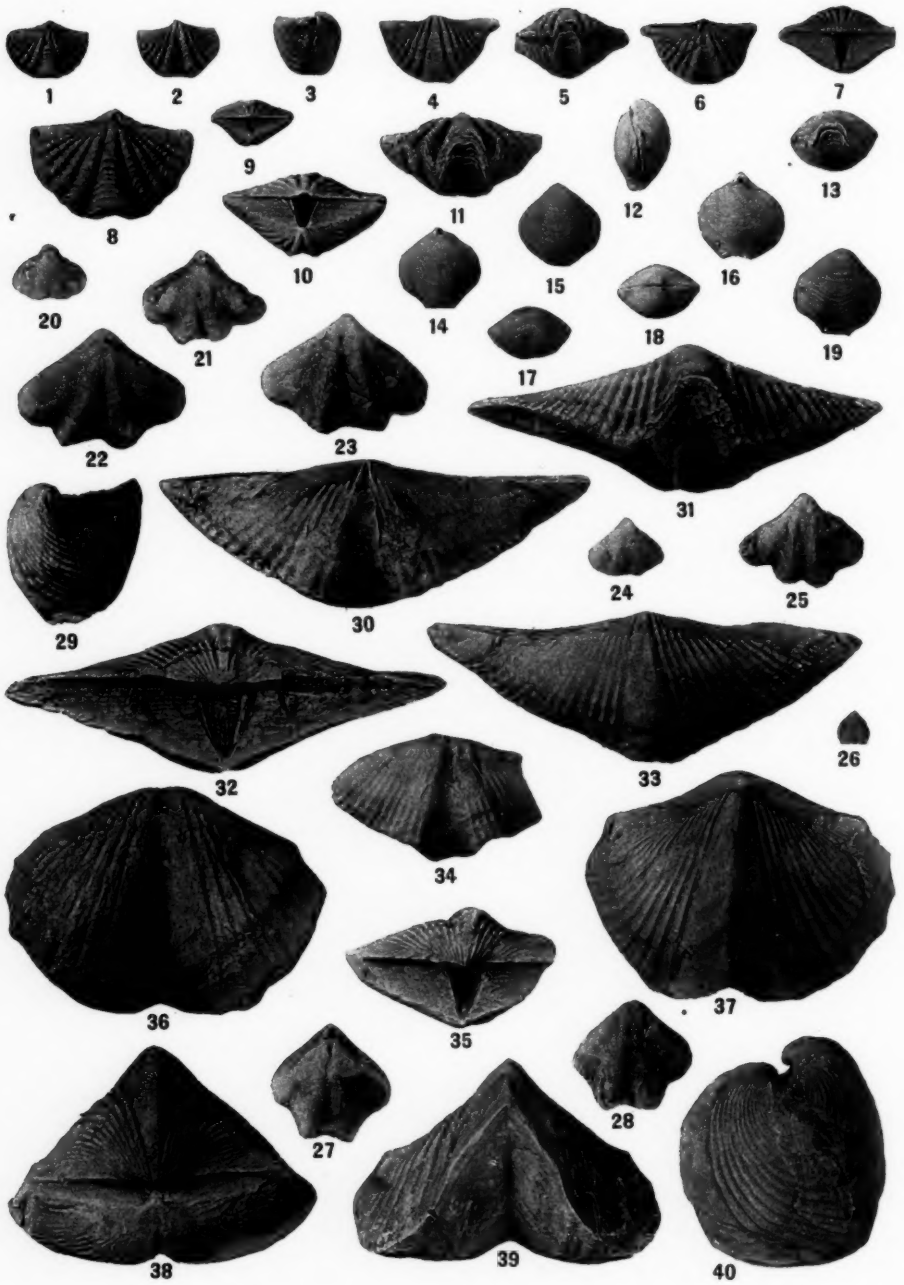
32–34—Chonetes mediolatus Cooper, n. sp. *32,* Ventral view of the holotype (U.S.N.M. 111651), ×1. *33, 34,* Ventral and dorsal views of two paratypes (U.S.N.M. 111652c, b plasticine replica), ×1. St. Laurent limestone (81 feet above base), 3 miles south of St. Marys, Missouri. (p. 480)

35–38—Chonetes scitulites Cooper, n. sp. *36,* Dorsal view of the holotype (U.S.N.M. 111658), ×1. *35, 37,* Dorsal and ventral views of the holotype, ×2. *38,* Dorsal interior, ×2, paratype (U.S.N.M. 111658a). St. Laurent limestone (near base), Devils Bakeoven, north of Grand Tower, Illinois. (p. 480)

44–46—Chonetes amplus Cooper, n. sp. *44, 45,* Ventral and dorsal views of two paratypes (U.S. N.M. 111663, a), ×1. *46,* Ventral view of holotype (U.S.N.M. 111656), ×1. St. Laurent limestone (277 feet from base of basal sandstone), St. Laurent Creek, 3 miles south of St. Marys, Missouri. (p. 481)



Cooper, Devonian Brachiopods



Cooper, Devonian Brachiopods

spondylium short, about 2½ mm. Dorsal median septum long, extending slightly anterior to the middle.

Measurements in mm.: holotype, length 10.2, width 11, thickness in median region 7.7, width of sulcus 6.6; paratype (Univ. Illinois D505a), length 8.5, width 8.8, thickness 5.5.

Holotype, University of Illinois D505; paratype, University of Illinois D505a; plastoholotype, U.S.N.M. 111654.

Horizon and locality.—Same as preceding.

For comparison with other species see *S. savagei*.

ATHYRIS NUCULOIDEA Cooper, n. sp.
Plate 64, figures 12–19

Shell fairly small for the genus, pentagonal to heptagonal in outline; posterior margins nearly straight and forming an apical angle of about 90°; lateral margins narrowly rounded and forming distinct shoulders; anterolateral margins sloping more or less strongly inward; anterior margin truncated. Length and greatest width about equal; greatest width located at about the middle. Surface lamellose in well-preserved individuals, lamellae short and crowded at the front margin.

Ventral valve moderately convex in lateral profile but with the greatest convexity located in the umbonal region; anterior profile broadly convex with the median region slightly flattened and the sides sloping fairly steeply. Sulcus narrow, occupying one-third to one-fourth the width, shallow and convex in cross section. Sulcus originating near the middle and bounded by two distinct, narrow, but inconspicuous folds that extend from the middle to the anterior margin. Tongue short, broadly rounded. Umbonal and median regions inflated; flanks convex and with steep sides. Beak rising above the dorsal umbo and slightly overhanging it. Foramen circular but with anterior lip resorbed.

Dorsal valve in lateral profile most convex in the umbonal region and with the anterior two-thirds flattened; anterior profile broadly convex and with the median area slightly inflated. Fold occupying about one-third the width and clearly defined for about one-third the length. Fold gently convex in section defined by two shallow lateral grooves. Flanks in posterior half sloping gently and evenly to the margins, gently convex in profile. Umbonal region swollen moderately, somewhat narrow.

EXPLANATION OF PLATE 64

FIGS. *1–11—Tylothyris bella* Cooper, n. sp. *1, 2, 9,* Respectively dorsal, ventral and posterior views of the paratype (U.S.N.M. 111670), ×1. *8, 10, 11,* Dorsal and posterior views of the paratype, ×2. St. Laurent limestone (*Microcyclus* bed), road to Alto Pass, center NE ¼ sec. 15, T. 12 S., R. 2 W., Unon County, Illinois. *3–7,* Respectively side, dorsal, anterior, ventral and posterior views of the holotype (U.S.N.M. 111671), ×1. Same horizon on Clear Creek, NE ¼ sec. 34, T. 11 S., R. 2 W., 1¼ miles southwest of Mountain Glen, Alto Pass Quadrangle, Illinois. (p. 488)

12–19—Athyris nuculoidea Cooper, n. sp. *12, 13, 16, 19,* Respectively side, anterior, dorsal and ventral views of the holotype (U.S.N.M. 111666), ×1. *14, 15, 17, 18,* Dorsal, ventral, anterior and posterior views of a paratype (U.S.N.M. 111667a), ×1. St. Laurent limestone, *Athyris* bed, small anticline just south of Union School, Altenburg Quadrangle, Illinois. (p. 485)

20–28—Anathyris quadrilobata Cooper, n. sp. *22, 23,* Dorsal and ventral views of the holotype (U.S.N.M. 108215a), ×2. *27, 28,* Dorsal and ventral views of a younger and more elongate paratype (U.S.N.M. 108215d), ×2. *21, 25,* Dorsal and ventral views of a young paratype (U.S.N.M. 108215b), ×2. *20, 24,* Dorsal and ventral views of a young, faintly lobed specimen (108215g), ×2. *26,* A very young paratype (U.S.N.M. 108215 1, now lost) without lobation, ×2. Callaway limestone, 2½ miles south of Clifton City, Missouri. (p. 486)

29–35—Brachyspirifer ventroplicatus Cooper, n. sp. *29–33,* Respectively side, ventral, anterior, posterior and dorsal views of the nearly complete but decorticated holotype (U.S.N.M. 111672), ×1. Limestone just below *Microcyclus*, Devils Oven, north of Grand Tower, Illinois. *34, 35,* Ventral and posterior views of two incomplete but well-lobed paratypes (respectively U.S.N.M. 111673b, a), ×1. Same horizon on creek 0.2–0.5 mile east of Union School, section 29, T. 35 N., R. 13 E., Altenburg quadrangle, Missouri. (p. 486)

36–40—Paraspirifer aff. *P. acuminatus* Cooper, n. sp. Respectively ventral, dorsal, posterior, anterior and side views of an exceptionally good specimen, (Univ. Illinois D2813), ×1. "Grand Tower" limestone, Jackson County, Illinois. (p. 487)

Ventral interior with small teeth, thickened delthyrial cavity defined anteriorly by a transverse callosity. Dorsal interior with small hinge plate but prominent posterior foramen.

Measurements in mm.: holotype, length 11.6, width 11.8, length of dorsal valve 10.2, thickness 7.9, width of fold at anterior margin 5; paratype, (U.S.N.M. 111667a) length 11.0, width 11.0, length of dorsal valve 9.9, thickness 7.3, width of fold at anterior margin 5.2.

Holotype, U.S.N.M. 111666; paratypes, U.S.N.M. 111667, a–d.

Horizon and locality.—St. Laurent (*Athyris* bed, 50 feet above the *Microcyclus* bed), near crest of small anticline, one-eighth to one-fourth mile south-southwest of Union School, southeast of Seventy-six, Altenburg quadrangle, Perry County, Missouri.

Remarks.—This species is characterized by its small size, short anterior fold and sulcus, and nearly equal length and width. In these respects it resembles *A. zonulata* Stainbrook but differs in having a more elevated and prominent ventral beak, somewhat more convex valves, and a narrower and more strongly elevated fold. *Athyris nuculoidea* also resembles *A. vittata brandonensis* Stainbrook but differs in its smaller size and less prominent fold and sulcus.

ANATHYRIS QUADRILOBATA Cooper, n. sp.
Plate 64, figures 20–28

Shell small, subrhomboidal in outline; wider than long; posterior margin forming an angle of 110° with the beak; lateral margins very narrowly rounded; anterior margin bilobed. Anterior commissure rectimarginate. Exterior marked by strong concentric lines of growth.

Ventral valve evenly and gently convex in lateral profile; broadly but gently convex in anterior profile. Umbo gently convex, beak moderately incurved. Foramen athyroid. Sulcus originating on the umbo and extending to the anterior margin, where it forms a median indentation separating lateral narrow folds bounding the sulcus. Folds separated from narrowly convex flanks by shallow grooves.

Dorsal valve slightly more convex and therefore a little deeper than the ventral valve. Folding as in the ventral valve, but unlike most American Paleozoic brachiopods, it is in the opposite stage, i.e., the ventral sulcus and lateral folds are opposite the median sulcus and bounding folds of the dorsal valve. This accounts for the strong anterior lobation.

Growth: The smallest specimen in the collection is 3 mm. wide by 2.5 mm. long and thus shows the transverse character of the species although the lobation is barely discernible. With increasing growth the lobation becomes more and more pronounced.

Interior: Few details of the interior were obtained as the specimens occur in a crystalline calcite matrix. Dental plates long and widely divergent. Dorsal hinge plate like that of *Athyris;* no median septum.

Measurements in mm.: holotype, length 8.2, width 11.8, thickness 4.5; paratype (U.S.N.M. 108215i), length 6.7, width 8.0, thickness 3.8.

Holotype, U.S.N.M. 108215a; paratypes, U.S.N.M. 108215 b–k.

Horizon and locality.—Callaway limestone, 2¼ miles south of Clifton City, Missouri.

Remarks.—This species differs from *A. helmersenii* (Verneuil) by its smaller size, wider median sulcus, and the more elongate anterior lobes. This is the first report of the genus in North America.

BRACHYSPIRIFER VENTROPLICATUS
Cooper, n. sp.
Plate 64, figures 29–35

Very wide, with the greatest width along the hinge and not quite 2½ times the length; crudely rhomboidal in outline; lateral margins nearly straight and sloping strongly toward the center. Surface costate, about 17 costae on each side of the dorsal fold.

Sulcus of the ventral valve originating at the beak, widening and deepening anteriorly to occupy about one-fifth the width. Sulcus narrowly concave in profile; tongue only moderately long but narrowly rounded. Sulcus bounded on each side by a prominent fold bearing four or five costae. Flanks on each side of these folds moderately steep and nearly flat in profile. Interarea long, very gently curved, and about procline in position. Posterior margins slightly concave and forming a beak having an apical angle of

about 120°. Delthyrium in length slightly more than 1½ times width.

Dorsal valve with fold moderately elevated above the flanks when viewed from the anterior side; fold narrowly rounded but with the top flattened slightly. Base of anterolateral extremities of fold with more or less strongly developed sulci corresponding to the folds margining the ventral sulcus. Flanks outside these dorsal sulci marked by more or less pronounced folds corresponding to the grooves defining the ventral folds. Remainder of flanks to cardinal extremities gently concave in profile and with gentle slopes. Dorsal umbo somewhat swollen and with the beak overhanging the ventral interarea.

Measurements in mm.: holotype, length 22.0, width 54.0, thickness 17.5, anterior width of sulcus 10, length of dorsal valve 18.9.

Holotype, U.S.N.M. 111672; paratypes, U.S.N.M. 111673, a, b.

Horizon and locality.—St. Laurent limestone (*Microcyclus* zone), Devils Bakeoven, north of Grand Tower, Illinois.

Remarks.—*Brachyspirifer ventroplicatus* can be recognized by its extended form and the more or less prominent folds bounding the sulcus of the ventral valve and the corresponding more or less deep sulci bounding the dorsal fold. It suggests *Spirifer perextensus* Meek and Worthen in the great lateral extension of the valves but differs in having a much longer ventral interarea and a narrower and more rounded fold. Meek and Worthen do not mention the strong folds and sulci bounding the fold and sulcus, which are such prominent features of the shell illustrated herein. These features also distinguish the species from *B. macronotus* (Hall) and *B. angustus* (Hall) of the New York Hamilton.

PARASPIRIFER aff. P. ACUMINATUS (Conrad)
Plate 64, figures 36–40

An unusually fine specimen of *Paraspirifer*, collected by Professor T. E. Savage from the limestone between the white crystalline beds of the Grand Tower limestone and the base of the St. Laurent limestone in the Devils Backbone section, has affinities with *P. acuminatus* (Conrad) and also with *P. bownockeri* (Stewart) from the Silica shale of Ohio. The Illinois specimen is intermediate between the two species but lack of additional specimens prevents assignment to a new species.

The Illinois shell has the following characters: about medium size for the genus, wider than long, with narrowly rounded sides and emarginate anterior margin. Ventral valve moderately and fairly evenly convex. Sulcus originating on the umbo, deepening anteriorly, and marked medianly by a narrow depression. Tongue long and sharp, forming an angle of about 75°. Flanks moderately convex; cardinal extremities deflected moderately in a dorsal direction.

Dorsal valve strongly convex in lateral profile, forming almost a right angle in anterior profile, with the sides almost flat. Fold moderately elevated, fairly strongly carinate and with steep sides. Flanks very slightly convex.

Measurements in mm.: length 31, width 43.7, thickness 28, width of sulcus 19?, hinge width 34.8.

Figured specimen, University of Illinois catalogue no. D2813; cast, U.S.N.M. 111653.

Remarks.—Compared with specimens of *P. acuminata* from the Falls of Ohio River the Illinois specimen has a much more carinate fold, proportionately wider hinge, and deeper but narrower sulcus. The Illinois specimen differs from a small example of *P. acuminatus* from Leroy, New York, in having a more elevated fold, a sharper fold, deeper sulcus, more rounded dorsal lateral profile and more dorsally deflected cardinal extremities. The measurements of the New York and Illinois specimens are very similar, but differences in the fold and sulcus are pronounced. The dorsal umbonal region of the New York form is flattened, thus giving it a different lateral profile, and the New York forms tend to develop large specimens with high, very carinate folds.

Paraspirifer bownockeri compared with the Illinois specimen has a less convex lateral profile and a fold that is equally or somewhat less carinate. The ventral cardinal extremities of the Illinois specimen are more deflected than those of the Ohio form. When viewed from the anterior, the tongue of *P. bownockeri* has straight sides, whereas that of the Illinois and New York specimens has a slight lateral lobation just before the

tongue narrows rapidly to a point. The ventral valve of the Ohio species also tends to a greater depth than that of the Illinois specimen.

The Illinois specimen has characters that link it to the Jeffersonville and Onondaga *P. acuminata* but at the same time it is also similar to *P. bownockeri*. This intermediate biological position may be a reflection of its stratigraphical location between the Onondaga (Grand Tower, sensu stricto) and the St. Laurent limestone, the base of which is close to the Silica shale horizon.

TYLOTHYRIS? BELLA Cooper, n. sp.
Plate 64, figures 1–11

Shell small, width varying from one and one-half to two times the length; hinge wide, cardinal extremities alate to mucronate; lateral margins moderately convex, sloping medially; anterior margin rounded to medially emarginate. Surface costate, six to seven costae marking the flanks. Entire surface lamellose, lamellae distant on the body of the shell but crowded anteriorly.

Ventral valve broadly hemipyramidal, unevenly convex in lateral profile, with the greatest convexity in the umbonal region; anterior flattened. Anterior profile broadly convex. Sulcus originating at the beak, narrow, deepening anteriorly but never very deep. Tongue short, narrow, truncated. Sulcus bounded on each side by a costa stronger than any of those on the flanks. Flanks gently convex, sloping moderately to the extremities, and depressed somewhat below the costae bounding the sulcus. Interarea more or less broad and flat depending on age, more or less curved near the beak; delthyrium longer than wide; beak gently incurved.

Dorsal valve in lateral profile flatly convex to moderately convex, with the maximum curvature located at the umbo; in anterior profile broadly and gently convex. Fold narrow, expanding slowly, anteriorly somewhat narrowly rounded but flattened on top and bearing a shallow median depression. Fold defined by moderately deep lateral grooves; flanks varying from gently concave to gently convex in profile.

Measurements in mm.: holotype, length 8.8, hinge width 15.9, midwidth 13.0, length of dorsal valve 8.8, thickness 8.8, width of fold at anterior margin 3.3?; paratype, length 7.8, width at hinge 11.0, midwidth 10.5, length of dorsal valve 6.5, thickness 5.7, width of fold at anterior margin 3.4.

Holotype, U.S.N.M. 111671; paratype, 111670.

Horizon and locality.—St. Laurent limestone (*Microcyclus* zone). Paratype from rotted limestone on west side of new road to Alto Pass about 1 mile north of Illinois State Highway 146, NE¼ sec. 15, T. 12 S., R. 2 W., Union County, Illinois. Holotype from Clear Creek just east of old bridge 1¼ miles southwest of Mountain Glen, NE¼ sec. 34, T. 11 S., R. 2 W., Alto Pass quadrangle, Illinois. Also from east side of north end of Devils Backbone.

Remarks.—This species differs from *T. varicosa* by its smaller size, less extended lateral extremities and more convex valves in the older adults. No species quite like it occur in the higher Middle Devonian.

CENTRONELLA NANA Cooper, n. sp.
Plate 63, figures 18–23

Shell small, subpentagonal in outline; posterolateral margins straight; lateral margins strongly rounded; anterior margin moderately convex. Anterior commissure strongly sulcate. Surface unornamented.

Ventral valve gently convex in lateral profile with the maximum convexity located slightly anterior to the middle. Anterior profile strongly and narrowly convex, with the sides sloping fairly steeply. Median region subcarinate but becoming somewhat flattened anteriorly toward the anterior margin. Flanks nearly flat and sloping at about an angle of 45°. Beak short, erect, revealing the deltidial area, and forming an apical angle of about 90°.

Dorsal valve fairly evenly convex in lateral profile but broadly concave in anterior profile. Umbonal region somewhat flattened and with the flanks flattened and sloping medially to the median depression. Anterior third geniculated anteroventrally to form a short tongue with narrow and truncated extremity.

Measurements in mm.: holotype, length 6.1, width 5.5, thickness 3.2.

Holotype, U.S.N.M. 111674; paratypes, U.S.N.M. 111677.

Horizon and locality.—Grand Tower lime-

stone, in branch of Darty Creek, 150 yards east of new Alto Pass Road, SE¼ sec. 10, T. 12 S., R. 2. W., about 4 miles northwest of Jonesboro, Illinois.

Remarks.—This small *Centronella*, which occurs in countless numbers in the lower Grand Tower limestone, was referred to *C. glansfagea* (Hall), but important differences exist between the two species aside from size. *Centronella glansfagea* is nearly twice the size of *C. nana* and has a very strongly incurved ventral beak, whereas *C. nana* has a small erect beak. This difference in the beaks makes *C. glansfagea* a strongly umbonate shell, but *C. nana* has a nearly flat umbo when viewed in lateral profile. The dorsal valve of *C. nana* is strongly geniculated ventrally in the anterior quarter and the remainder of the valve is more broadly sulcate than that of the Schoharie shell. In anterior view the ventral valve of *C. nana* is broadly plicate, but the anterior commissure of *C. glansfagea* varies from nearly rectimarginate to moderately plicate.

MANUSCRIPT RECEIVED AUGUST 2, 1944.

JOURNAL OF PALEONTOLOGY, VOL. 19, NO. 5, PP. 490–503, PL. 65, 1 TEXT FIG., SEPTEMBER 1945

A BELEMNITE FROM A MISSISSIPPIAN BOULDER OF THE CANEY SHALE

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ABSTRACT.—The new genus and species *Eobelemnites caneyense* is described from a specimen from a boulder, evidently Mississippian in age, from the Johns Valley (Caney) shale of Oklahoma. Preservation of this form is such as to permit a close study of the phragmocone, bringing out for the first time the presence of such structures as the septal furrow and cameral deposits in belemnoids. These features persist into much higher forms. Comparison with other belemnoids is made difficult owing to uncertainty as to the relative values of the several classifications proposed, and owing to uncertainties as to structural features of some crucial Mesozoic species. However, *Eobelemnites* appears to unite the Protobelemnitidae and Eubelemnitidae if the criteria of these groups are valid. The genus shows no features which present a clue to the precise origin of the Coleoidea, but it indicates that the coleoids were differentiated much earlier than was previously believed.

INTRODUCTION

THE Coleoidea (Dibranchiata) have previously been known from Mesozoic and Tertiary strata, with the addition of a few forms of upper Permian age. The present study is primarily devoted to the description of a belemnoid from a boulder, evidently of Mississippian age, from the Johns Valley (Caney) shale of Oklahoma. Surprisingly, this form does not seem to be strikingly primitive, for it possesses rostral and proostracal features that are essentially those of the Belemnoidea. Such features of the phragmocone as suggest orthoconic nautiloids are those which are retained in higher and younger belemnoids and are therefore not indicative of the primitive condition of this species. Comparison with described Mesozoic belemnoids revealed, however, a number of facts, some new, and some which are briefly outlined here inasmuch as they involve a survey of investigations which do not seem to be at all well known in this country. The older belemnoids of the Mesozoic have been placed, except when the rostrum shows prominent surface markings, in *Atractites*. An investigation of that genus was undertaken, the results of which presented so many ramifications irrelevant to the present discussion that they are published separately. Briefly, however, the genotype, *A. alpinus* Gümbel is so inadequately known that no other species can be placed in *Atractites* with certainty. Among the better-known species formerly included in *Atractites*, one group of forms is characterized by a slender pauciseptate phragmocone, a long rostrum, and a well-defined proostracum. For these species the genus *Ausseites* is proposed, which is regarded as having essentially the scope of *Atractites* as used by most European investigators. Hyatt and Smith (1905) presented a very different concept of the genus, colored largely by features which they observed in *Atractites philippii*. The new genus *Metabelemnites* is proposed for this form, which appears to be a primitive member of the family Diploconidae (Naef, 1922) in which there is a progressive reduction in the size of the rostrum, which also loses its generalized structure of aragonitic fibres, and the proostracum becomes small and conchiolinous. Prior to this investigation the writer had accepted the concept that among the earlier belemnoids commonly placed in *Atractites* there were forms such as had been represented diagrammatically by Dunbar (1924) combining a rostrum with a normal nautiloid living chamber. However, while clear evidence as to the condition of the anterior end of the shell is wanting for many species, there is no basis for assuming the existence of any such condition among Mesozoic species. Conothecal striae have been found among the earlier *Ausseites* (Zittel, 1885) as well as in other Aulacoceratidae. Although among members of this family the conotheca continues orad

of the last septum of the phragmocone for a short distance, sometimes suggesting the base of a normal living chamber, the conothecal striae found in such species indicate that the proostracum is well developed. Further, it was found that this aseptate condition of the anterior end of the conotheca is a condition not by any means confined to the older and more primitive of the Belemnoidea.

Unfortunately attempts to correlate the present species with the classification of the belemnoids has not been altogether successful. This has been largely due to uncertainty as to what classification should be accepted, for while a number of very marked improvements over the older classifications of Zittel (1885) and Hyatt (1900) have been made by European students, the more important of which are noted below, it is unfortunately not possible to evaluate the relative merits of these several schemes, partly because of lack of concise definitions, partly because they do not explain clearly why earlier schemes have been rejected, and partly because of uncertainty of some of the morphological conclusions involved. Belemnoid remains are typically fragmentary, and it does not seem that the extant data are sufficient to warrant the broad generalizations which have sometimes been proposed.

ACKNOWLEDGMENTS

The writer wishes to express his thanks to the U. S. National Museum and Dr. Ray S. Bassler for the loan of the specimen described here, as well as much other cephalopod material. Dr. J. B. Reeside has kindly supplied suggestions in connection with the search for more information concerning the genotype of *Atractites* and has permitted the examination of American and European coleoid material. An adequate investigation of the literature would not have been possible without the cooperation and courtesy of the Academy of Natural Sciences of Philadelphia. For such courtesies I am indebted to Dr. Charles M. B. Cadwalader, Dr. B. F. Howell, Dr. Horace G. Richards, and to members of the library staff. Photographic equipment and facilities were supplied by the University of Cincinnati Museum, where also a large collection of belemnoid material aided the investigation materially.

Genus EOBELEMNITES Flower, n. gen.

Genotype, *Eobelemnites caneyense* Flower, n. sp.

Conch belemnoid. Phragmocone large, compressed, with a relatively large apical angle. The septa are relatively closely spaced, the sutures oblique, sloping orad from venter to dorsum. In the early portion of the genotype faint lateral lobes modify the sutures. These lobes lie in line with the asymptotes of the conotheca. The septum is typical, complete with the mural part, and a normal septal furrow on the dorsum. The septal necks are relatively long and flare slightly at their tips. The connecting ring was fragile, and possibly originally incomplete, forming segments which were faintly fusiform in outline. Vestigial mural deposits occur in the camerae.

The conotheca consists of certainly two and possibly three layers, the outer one of which bears the conothecal striae and very fine numerous longitudinal lines. The conothecal striae indicate a well-developed dorsal proostracum with a thickened axis. Those of the dorsum are separated from the asymptotic bands by prominent linear ridges. The asymptotic bands are not sharply set off from the ventral region, but reverse their curvature, forming a broad, low crest over the venter.

The rostrum is typical in its radially fibrous composition. It is faintly compressed in section, slightly thicker on the ventral side of the phragmocone than on the dorsal side, and contracts slightly apicad in the known portion. Its adapical portion is missing, and it may have extended far apicad of the protoconch, and may or may not have developed a faintly clavate tip as in many Aulacoceratidae. The surface of the rostrum as such is not exposed. Its cross section shows that in the region of the phragmocone there are no prominent grooves or furrows of appreciable relief. What may represent the thinning adoral edge of the rostrum attached to the conotheca shows a smooth, unstriated surface, which shows shallow pitting under the microscope. The proostracum is unknown, but its form is inferred from the conothecal striae. The phragmocone is large, and only its adapical half was enclosed by the rostrum.

Discussion.—This genus differs from most Aulacoceratidae in the relatively rapid ex-

pansion of the phragmocone, the shallow camerae, and the markedly oblique sutures. These features are found instead in the more specialized belemnoids, the Eubelemnitidae of Pavlow (1913), and von Bülow-Trummer (1920). However, the development of a crest in the conothecal striae on the venter is a feature which these authors have accepted as one confined to and characteristic of the aulacoceroids, although the evidence is incomplete and perhaps questionable for such a broad generalization. Species which have been placed in *Atractites* in the past, agree rather closely with *Eobelemnites*. However, among these species those typical of *Ausseites* have generally more slender and less closely septate phragmocones. The monotypic *Metabelemnites* possesses a phragmocone which ends in a blunt tip just apicad of the tip of the phragmocone. While we can only infer that this is not true of *Eobelemnites*, the genera differ further in that *Metabelemnites* fails to retain the usual radial fibres in the interior of the rostrum. Additional differences in the proportions and shape of the phragmocone and rostrum leave little close resemblance between the genera. A few anomalous species, for lack of a better resting place, might be tentatively retained in *Ausseites*, which exhibit phragmocones that are atypical in the wider apical angle or the more closely spaced septa or both. None, however, resemble *Eobelemnites* strongly in the close spacing of the septa, though a few develop more rapidly expanding conothecae. The best known of such species are *Atractites conicum* and *A. convergens*. (See von Mojsisovics, 1902, pls. 15, 16).

Unhappily, while much is known concerning the phragmocone of *Eobelemnites*, little is known concerning its rostrum. The genera of the Eubelemnitidae are determined largely upon the basis of the features of the surface of the rostrum. However, a much closer comparison with the higher belemnoids is possible on the basis of the extant data. Possibly the most important difference is found in the conothecal striae. As members of the Eubelemnitidae, these coleoids lack any indication of a crest on the venter, which would be clearly known from the condition of the conothecal striae. Happily the conothecal striae have been studied and illustrated for the more crucial of the genera of the Belemnitidae using the family name in the sense in which it has been employed by Naef (1922), rather than in the more restricted sense in which it was used by Stolley (1919) and others. The rate of expansion of the phragmocone, its cross section, the slightly oblique sutures, and the spacing of the camerae suggest rather strongly the phragmocones of the earlier Jurassic belemnoids. However, none of these forms are known to show the "asymptotic" lobes which characterize the early growth stages of *Eobelemnites*. *Cuspeteuthis* and *Holcoteuthis*, which are most similar to *Eobelemnites* in general aspect, differ in features that are not generally described in discussions of the genera, where rostral characters are mainly considered. Both genera differ from *Eobelemnites* in the curved dorsal profile of the phragmocone, which is particularly marked near its apex. *Dactyloteuthis* has a phragmocone more similar in shape to *Eobelemnites*, but the rostrum is thick, short, and massive, the phragmocone is not known to extend orad of the rostrum as in *Cuspeteuthis* and *Holcoteuthis*. In most other genera the phragmocone fails to extend orad of the rostrum, and in some the phragmocone is confined to the adapical part of the alveolus within the rostrum, where the septa appear to become progressively more crowded and more tenuous until they finally disappear, leaving only the mural parts of the septa, which are responsible for the annulated appearance of alveoli even in Tertiary coleoids.

Eobelemnites combines the rapidly expanding and multiseptate phragmocones of the Eubelemnitidae, though with a degree of calcification of both the conotheca and septa which is rare in this group, with the conothecal striae reported in the Aulaceratidae. As such, it is typical of neither family but distinct from the genera included in both groups.

EOBELEMNITES CANEYENSE Flower, n. sp.
Plate 65, figures 1–5; text figure 1

This species is known only from the holotype, a phragmocone retaining some portions of the rostrum, the entire specimen being 98 mm. in length. The extreme apical part of the phragmocone, estimated at 8

mm. in length, is missing. The basal 45 mm. of the extant part is undistorted and beautifully preserved, but the adoral portion, 45 mm. in length, is badly crushed. The prostracum is unknown, and the phragmocone may not be complete adorally. The undistorted part of the phragmocone is compressed in section, expanding from 5½ mm. and 7 mm. to 18 mm. and 20 mm. in the length of 45 mm. The 23 camerae in this length increase from 1 mm. to 3 mm. in depth as they are traced orad. A slight but noticeable abrupt increase in the depth of the camerae occurs beyond the fourth extant suture of the holotype, but the increase is otherwise gradual and uniform.

The sutures are markedly oblique, sloping orad from the venter to the dorsum. Adapically the sutures form a broad lobe on the venter. The ascent of the sutures dorsad is interrupted by a pair of small shallow lobes on the dorsolateral region, in line with the asymptotes of the conotheca. Dorsad of these lobes, the sutures are nearly straight and transverse. Adorally the asymptotic lobes are lost and the obliquity of the suture is more uniform.

The siphuncle is small, lying close to but not quite in contact with the ventral wall of the conotheca. It has been exposed by grinding in the adapical 15 camerae of the holotype, by a slightly oblique section ground from the ventral side (pl. 65, fig. 1, text fig. 1A). The septal necks of the adapical four camerae are rather abruptly bent, their tips diverging slightly apicad, so that the condition is almost cyrtochoanitic. At a glance these necks appear to be considerably thicker than the free parts of the septa of which they are only bent continuations (fig. 1A). Closer examination, however, shows that the apparent thickening is due to the addition of a layer of dark-brown material, rather thick, and presenting a suggestion of irregular spongy structure in opaque section. This material appears to represent a vestige of the connecting ring. The necks in the first four camerae are slightly less than half the length of the camerae themselves. In the next few camerae, which are perceptibly deeper, the same relationship holds. In the twelfth to fourteenth camerae the septal necks appear to be considerably longer. Here the segment expands apicad of the septal foramen, but the apical ends of the preserved part of the segment tend to approach each other apicad, forming a suggestion of a slender nummuloidal or fusiform segment, similar to that figured for "*Ausseites*" *ausseanus* and *A. conicum* (von Mojsisovics, 1902). Closer examination shows that even here the necks are about half the length of the camera, and the remainder of the segment is made up of the relatively dark spongy material of the connecting ring. The interior of the camerae is occupied by infiltrated material, and no matrix is present. This shows that the connecting ring was originally a very weak structure, and that its incomplete condition may have been original rather than due to subsequent destruction.

The free part of the septum is smoothly and only slightly curved, the curvature being greatest at the most adapical portion. The most adoral part of the septum, found on the dorsal side, is scarcely curved.

The surface of the phragmocone is preserved with remarkable clarity, and several distinct layers of its wall are exposed by exfoliation. The innermost of these layers, shows the wall of the camera to consist of two distinct regions. Apicad there is a narrow unpolished zone, which appears to be at a slightly deeper level than the other layer (text fig. 1A, d). The remainder, occupying the greater part of the length of the camera, lies orad of this and shows a polished surface with many fine longitudinal markings.

The unpolished zones lying at a deeper level are slightly thicker on the venter than on the dorsum, but are missing in the midventral region causing the median feature shown in plate 65, figure 5, simulating a ventral saddle of the suture. This suggests at once the circumferential distribution of cameral deposits as noted in the Pseudorthoceratidae (Flower, 1939, p. 36–38). Such an interpretation is confirmed by inspection of the exterior of the phragmocone adjacent to the unpolished section (text fig. 1A). Here the septum shows a broken surface on the exterior. It evidently extended farther distad than the region now preserved, before it joined the shell wall and projected orad forming the mural part of the septum. The unpolished zone represents the surface of a

structure which was independant of the true septum and lay on the inner or cameral surface of the septum at the region of the suture. The distribution of this layer, as inferred from the impression of its surface, agrees with that of the cameral deposit as known from the Pseudorthoceratidae and many other, though not all orthoconic nautiloids. Further, this layer is slightly thicker and considerably more deeply impressed in the adapical camerae than in the adoral length from one suture to another. Their presence in some parts of the phragmocone as only modifications of color inside the replaced shell, indicates that the mural part of the septum is actually retained on the surface of the exfoliated specimen in some regions, but it is so thin that its presence cannot be detected otherwise. It has been impossible to distinguish between parts of the specimen showing only the impression of the inner surface of the mural part of the

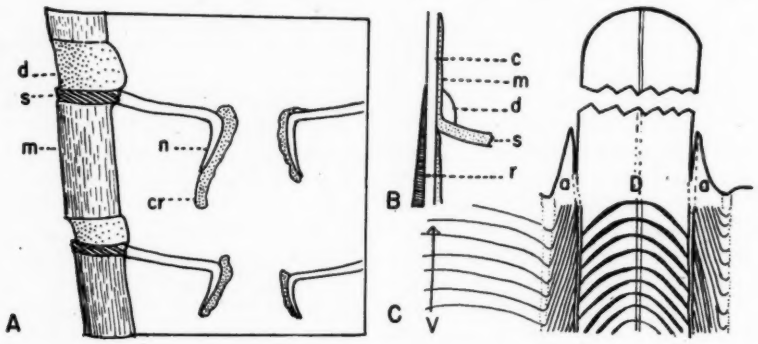

FIG. 1—*Eobelemnites caneyense* Flower, n. sp. Details of morphology.

A, Part of phragmocone showing natural exfoliated surface on left, artificially ground section on right, exposing siphuncle. *d*, Non-striated dull zone representing mold of cameral deposit; *s*, septum, showing broken edge at surface of specimen; *n*, septal neck; *cr*, connecting ring; *m*, polished and finely striated surface internal mold of mural part of septum.

B, Reconstructed cross section through wall of phragmocone. *c*, Conotheca or conch; *r*, rostrum; *m*, mural part of septum; *s*, free part of septum; *d*, cameral deposit.

C, Projection of conothecal striae. *V*, Venter; *D*, dorsum. The relative thickness of the lines is designed to indicate their relative clarity. *a*, Asymptotes. Above the dorsum the outline of the rostrum is reconstructed. This is broken since it is impossible to estimate its actual length. The reentrants dorsad of the asymptotes are dubious.

part of the phragmocone. These facts confirm the interpretation of the structure as a true cameral deposit. Further confirmation can be found in a few places on the shell where the polished striated surface may be seen to continue over this area, and where the shell is so transparent that this extra shell layer can be seen obscurely beneath it, as interpreted in text figure 1B.

The striated and highly polished surface represents either the outer or the inner surface of the mural part of the septum, which is evidently very thin here. That this layer extends orad of each suture for the length of a camera is shown by the persistence of the septal furrows on the dorsum. These extend almost, but not quite the entire septum, a condition which is evidently present in the venter adjacent to the polished section, and portions retaining the mural part of the septum itself and therefore showing its outer surface which was originally in contact with the conotheca. Both show similar polished and striated surfaces.

On the middorsal region of the conch the septal furrow may be recognized. Here, as in the nautiloids, it represents a middorsal region in which the mural part of the septum is not secreted. Where the septum is exposed by exfoliation, the dorsal furrow is faintly but distinctly outlined by a fine suture. Where it is covered by other shell layers it can be detected through them owing to the transparent nature of the shell layers in

their present condition.

Outside the polished layer there are two and possibly three other shell layers. The inner two are essentially identical in their surface features. They show a faintly polished surface bearing minute irregular and faintly rugose transverse markings, in general faintly oblique and apparently parallel to the oblique course of the sutures. There may be seen here also very faint reflections of the conothecal markings which are best expressed on the outer layer discussed below. It is possible, though unlikely, that only one such layer may be actually developed, and that the appearance of similar surfaces at two different levels might be the result of very slight crushing.

The outer layer, also faintly polished, shows the type of sculpture known on the conotheca of other belemnites, consisting of conothecal striae and some accessory ornamentation, largely of fine longitudinal markings. These lines are regarded as homologous to the lines of growth of nautiloid shells and reflect the shape of the anterior edge of the shell, the rostrum. The form of these striae is shown in plate 65, figure 2 in dorsal view, and they may be seen also, though more obscurely in figures 3 and 6. A diagrammatic projection of these striae is shown in text figure 1C, with a reconstruction of the form of the proostracum shown above the dorsal portion. Broad forward-projecting arcs are formed on the dorsum and centered upon a continuous middorsal ridge, which resembles the conchial furrow of nautiloids but probably has nothing to do with the conchial furrow, which is a ventral and not a dorsal structure. Instead, its homologies are to be found in the slight axial thickenings of the rostrum in many Coleoidea including the living *Loligo*. The dorsal area is bounded by two prominent longitudinal ridges separating the dorsum from the asymptotic bands. These ridges are of uncertain interpretation in reference to the form of the rostrum. They may represent regions in which the growth lines of the rostrum assume a longitudinal position. On the other hand, they may, as suggested in the text figure, indicate reentrant regions such as have been found in some higher Coleoidea (Naef, 1922, p. 172, fig. 65a, b). A simpler interpretation has generally been offered, and it has been assumed that the older belemnites showed no such reentrant regions. However, the proostraca are actually preserved in only a very few of the Belemnitidae, and none are known for the Triassic genera commonly assigned to the Aulacoceratidae. The asymptotic bands are essentially similar to those of other belemnoids, the lines becoming progressively steeper from the ventral to the dorsal side. No clear ridge marks the ventral boundary of the asymptotic zones. Instead, the bands reverse their curvature in clearly defined though minute hooklike impressions and continue over the entire ventral region, forming a low, broad crest. The conothecal markings are very obscure ventrally where the longitudinal markings of the surface become larger and more prominent, as can be seen from the upper part or plate 65, figure 1. No keel or ridge occupies the midventral surface of the conotheca nor can any trace of a conchial furrow be seen there. The fine longitudinal lines and the striae on the adoral surface of the conotheca are replaced by a minute pitted and faintly vesicular pattern such as is commonly found on the surface of the smooth rostra of belemnites, and which may represent the thinning anterior edge of the rostrum retained on the surface of the conotheca.

Of the rostrum, which has supplied the features used most widely for the classification of belemnite genera, relatively little is known. It is obviously faintly compressed in section. It is slightly thicker on the ventral side than on the dorsal side of the phragmocone. Its surface is nowhere exposed, except possibly as noted above on the conotheca. Its broken apex shows a cross section adequate to indicate that there are no prominent ridges or grooves in the region of the phragmocone.

The extant portion of the rostrum tapers, contracting very slightly apicad. In a length of 10 mm. it contracts apicad from 14 mm., where the enclosed phragmocone is 12 mm. in diameter, to 13 mm., where the enclosed phragmocone is reduced to 7 mm. The adapical contraction is uniform in the known portion of the rostrum, which does not extend, however, even to the tip of the phragmocone. Adorally the rostrum thins to a narrow edge commensurate with the uncrushed portion of the phragmocone.

Evidently the support of the rostrum, rather than any inorganic factors, was responsible for the uncrushed condition of the apical part of the phragmocone. The broken portion of the rostrum shows clearly the usual internal structure of radiating aragonitic fibres. The apex of the rostrum is missing. There is no evidence as to whether it was short and blunt or whether it may have been long. The extant portion is similar in its proportions to the rostrum of *Aulacoceras*, which extends far apicad of the phragmocone and is expanded into a narrow club before contracting finally to its tip.

Discussion.—Although this investigation is the first to point out the presence of the septal furrow, the mural part of the septum, and the cameral deposits in belemnoids, the appearance of these features in *Eobelemnites* does not indicate that it is primitive, for they are features which can be recognized on much younger and more advanced belemnoids. Phillips (1865, p. 23, diagram 13), has figured structures similar to the septal furrow. He regards these as ventral, apparently on the basis of a specimen which lacked true septa, and interprets them as markings caused by the point of contact of the septal neck with the wall of the shell. However, the writer has had ample opportunity to observe the presence of the septal furrow on the antisiphonal side of many British and European belemnoids in the collections of the University of Cincinnati Museum.

The siphuncles of belemnoids have not been studied for a very large number of species. However, von Mojsisovics (1902, 1871, 1882), has figured a large number of siphuncles quite similar to that of *Eobelemnites* in various species of *Aulacoceras*, and in species which he placed in *Atractites*, most of which will join *A. ausseanus* in the genus *Ausseites* Flower. One of these forms shows complete siphuncular segments with complete connecting rings in addition to the rather long septal necks, producing slender fusiform segments. *"Atractites" conicum* (von Mojsisovics, 1902), has considerably more inflated segments. Phillips (1865, 1867), has figured a number of siphuncles of more specialized belemnites, largely from the Lias, which sometimes fail to agree closely with our material. *Belemnites gigensis* (Phillips, pl. 5, fig. 11), is represented as possessing a strongly nummuloidal siphuncle in which the distinction between the septal necks and the connecting rings is unfortunately not recognized. This species is currently placed in the genus *Homaloteuthis*. *Belemnites ilminstrensis* (Phillips, 1867, pl. 12), now included in *Cuspeteuthis*, is represented as having long septal necks without connecting rings, not unlike those of *Eobelemnites*. The same species shows traces of the septal furrow on the dorsum. This, and other species as well, frequently show in addition molds of cameral deposits identical with those seen on the exterior of the phragmocone of *Eobelemnites*, though Phillips (1967, pls. 20–22), has interpreted them on quite a different basis, regarding the septum as bifurcating as it approaches the shell wall and sometimes as thickening there. Careful examination of several phragmocones of Jurassic species has made it necessary for the writer to reject this interpretation, and removes the possibility that these younger forms might have developed modifications of septal and cameral structures which might supply differences between the older and the younger representatives of the belemnoids. Further, the persistence of the septal furrow on the dorsum in some of these same forms can only mean that the mural part of the septum was present, though doubtless extremely thin, over the entire length of the wall of the camera. There is, then, no essential change in the structure of septa among the belemnites as long as a normal calcified septum is retained. There seems, however, to have been considerable variation in the form of the segments of the siphuncle, though the slender fusiform segments seen in *Eobelemnites* appear to have been the commonest type.

The similarities and differences shown by the phragmocone and the conothecal striae have already been discussed at some length in connection with the generic description. The pattern of the proostracum is essentially that reported for the Aulacoceratidae by von Bülow-Trummer (1920), while the shape of the phragmocone suggests instead the Belemnitidae. No illustrated phragmocones in the Aulacoceratidae are at all closely similar to that of *Eobelemnites* in proportions. However, among the older and apparently more primitive of the "tribe"

Eubelemnitidae, phragmocones closer to that of *Eobelemnites* occur. The only two species definitely known to have similar phragmocones which protrude well orad of the rostrum are *Cuspeteuthis ilminstrensis* (Phillips, pl. 12), and *Holcoteuthis elongatus* (Miller) (see Phillips, pl. 7). These genera have been placed by von Bülow-Trummer and Stolley in the Polyteuthidae, regarded as the most primitive family of the true belemnites, characterized, among other features, by the absence of an embryonal rostrum.

Type.—Holotype, U. S. National Museum.

Occurrence.—The holotype originally bore a label reading "*Loxoceras* (?) boulder in Caney shale. Oklahoma. E. O. Ulrich." As the boulders in the Caney shale carry faunas ranging throughout a considerable part of the Paleozoic it seemed that the horizon could not be very well established. However, not only the faunas but also the lithologies of the various age groups have been clearly described by Ulrich (1927, 1927A). Happily the matrix of *Eobelemnites* is consistent with the description of only one age group of boulders, that of middle Mississippian age as indicated by the fauna described by Girty (1909). Ulrich describes such boulders, which he states are the most abundant ones in the Caney, as follows: "Loose and usually small but slightly waterworn pieces of bluish-gray calcareous shale and calcareous nodules." The exact age of these boulders and therefore the exact age of *Eobelemnites* will of course depend upon estimates based upon other members of the fauna. The generally accepted correlation of these boulders is with the Meremac group, and probably the St. Louis limestone.

DEVELOPMENT OF THE COLEOIDEA

Dunbar (1924, pp. 219–221), has proposed a series leading from a straight nautiloid shell to a typical belemnite. The beginning of the series, indicated as *Orthoceras*, is a simple, straight, external shell with a subcentral tubular siphuncle. This leads to "*Atractites*" which is characterized by the enclosure of the mantle over the shell and the secretion of a small rostrum. The living chamber is unmodified, and the phragmocone is changed only by the migration of the siphuncle to a ventral position. The third step, indicated as *Belemnites*, shows an increase in the size of the rostrum, a widening of the apical angle of the conotheca, a crowding of the septa, and the loss of the conotheca, the original shell wall, orad of the phragmocone except for a portion on the dorsum, which becomes the proostracum.

Unfortunately for this theory, there seems to be no such creature as Dunbar represents for *Atractites*. The known Aulacoceratidae had already developed well-specialized and according to Pavlow (1913), von Bülow-Trummer (1920), and Naef (1922), rather distinctive proostraca. *Atractites*, as elsewhere noted (Flower, 1944) is a genus which cannot be recognized. The European species which have been assigned to it are placed by the writer in *Ausseites*, a new genus based upon *Atractites ausseites* Mojsisovics. This name, designed to replace *Atractites* as used by Mojsisovics and most subsequent European authors, includes shells which differ from Dunbar's concept of the genus not only in possessing no true living chamber, but also in that the rostrum is always long, massive, and much larger than the phragmocone.

The developmental trends of the earlier Mesozoic belemnoids which can be inferred from the stratigraphic relationship of the various morphological groups, fail to support the concept of a gradual orthogenetic progression in the increase in size of the rostrum. The earliest forms are referred to the Aulacoceratidae, shells with appreciable phragmocones, it is true, but also with rostra which extend far apicad of the phragmocone and are well calcified and frequently massive. Aulacoceroids are known throughout the Triassic and persist into the Liassic. They have also been recognized in the Permian, where, however, they are rather poorly known.

By Upper Triassic time two additional stocks have appeared, both of which are characterized by a reduction in size of the rostrum and a tendency toward the replacement of the originally aragonitic shells by conchiolinous material. The appearance of the Belemnoteuthidae in the Keuper marks a line which is already quite highly specialized by the reduction of the rostrum to a thin conchiolinous sheath for the phragmo-

cone, while the proostracum remains strongly calcified and aragonitic. This line, according to Zittel (1885) and Hyatt (1900), persists into the Cretaceous. Naef (1922) regards the forms which were formerly included in the Belemnoteuthidae as constituting several different families.

The second line of descent showing a similar shell reduction is the Diploconidae. *Metabelemnites* Flower of the upper Triassic and *Diploconus* of the Jurassic also show a reduction of the rostrum but fail to indicate that it has become conchiolinous. Instead, the proostracum has apparently been changed from aragonite to conchiolin in *Diploconus*. It has not been observed in the older *Metabelemnites*.

Clearly, the Belemnoteuthidae and the Diploconidae require as a common ancestral type a well-calcified belemnoid shell with well-developed phragmocone, proostracum, and rostrum, just such shells as are found in the Triassic before these families appear. Unfortunately for Dunbar's interesting hypothesis, its author was apparently not familiar with the existence of conothecal striae in these earlier Triassic forms, although the structures had been figured by Zittel (1885), and discussed by Stolley (1918), von Bülow-Trummer (1920) and Naef (1922) and applied to the classification of these shells rather extensively.

In spite of the lack of any evidence in the Mesozoic for cephalopods with straight shells and unmodified living chambers, the existence of such an organism is not at all improbable. The conothecal striae observed in the Aulacoceratidae of the Mesozoic preclude including such a shell in that family. The presence of similar striae, though with a slightly different pattern on the dorsum, in the Belemnitidae (sensu lato) precludes placing such a form there. The presence of *Eobelemnites* in the Mississippian shows that by that time the proostracum was already highly specialized; more, the proostracal pattern attributed to the Protobelemnitidae (or Aulacoceratidae) was perfected in this form. Clearly any ancestral belemnoid retaining a nautiloid living chamber must be sought in earlier strata.

While it is generally believed that the Coleoidea must have arisen from cephalopods with straight external shells, the precise connection has not yet been established. The present evidence suggests more than one possible connection, and in the hope of stimulating interest in the problem, some of the possible interpretations are outlined here together with some of the objections which make them unsatisfactory, at least in the light of our present knowledge.

Perhaps most intriguing is the problem as to whether the Coleoidea arose from a typical nautiloid ancestor such as was formerly called *Orthoceras*, or whether it arose from the perplexing genus *Bactrites*. Several lines of evidence seem to support the possibility that the coleoids may have sprung from a *Bactrites*. The phragmocones of the earlier Mesozoic species are slender, the chambers are widely spaced, the siphuncle is marginal, and its septal necks are relatively long. In short, the shell pattern is essentially that of a *Bactrites* insofar as the phragmocone is concerned. The presence of a small protoconch embedded in the rostrum at the apex of the phragmocone, which appears to be a universal feature of the belemnoids, also suggests an origin in *Bactrites*. Furthermore, possible ancestors of the coleoids are found in Pennsylvanian and Permian species, known only from phragmocones, which have been assigned to this genus. As such shells are known rather imperfectly, it is even possible that they may have been internal. Indeed, these phragmocones alone usually fail to show any characters by which they could be separated with certainty from comparable fragments of Triassic species formerly included in *Atractites*.

Closer scrutiny of the problem reveals that this interesting possibility is not suggested by all of the evidence. The protoconch of the belemnoid suggests an origin in *Bactrites* but is not in itself conclusive. It is known that normal orthoceracones had a small poorly calcified protoconch, which was lost later in life. If in such a shell the mantle enclosed the shell wall and secreted a rostrum upon it, such a process must have taken place in a very early growth stage. This process would cause the protoconch to be calcified and preserved, even though it were not retained through life in the ancestral form.

The slender form of the shell and the

widely spaced septa, even if significant, need not suggest *Bactrites*. Similar shells were developed in nautiloids, notably in "*Orthoceras*" *arkonense* Whiteaves, of the Middle Devonian of Ontario, Indeed, it is uncertain whether some species currently placed in *Bactrites* may not have been derived from this form.

Eobelemnites, however, lacks the extremely slender phragmocone and extremely widely spaced septa of most of the Aulacoceratidae, and suggests that these features may not be primitive. The possibility must be considered that the slender and sparsely septate shells found in most Aulacoceratidae may represent a specialized rather than a primitive condition. Further, the well-developed rostrum and conothecal striae show that the belemnoid pattern was well established by Mississippian time and that simpler types must be sought in much earlier strata.

CLASSIFICATION OF THE COLEOIDEA

The classifications of the Coleoidea that have appeared in the last 50 years vary radically. Some differences are nomenclatorial, as may be expected, but others involve fundamental differences of opinion as to the taxonomic significance of the various structures involved. The term Coleoidea, proposed by Waagen to replace the older term Dibranchiata, is adopted here inasmuch as there is no certainty as to where in the cephalopod development leading to recent squids and octopi, the presumably primitive four-gilled condition known in *Nautilus* and assumed to apply to all Nautiloidea and Ammonoidea, gave way to the two-gilled condition that characterizes all living cephalopods in which the shells are internal or wanting.

There is likewise much difference of opinion as to the major divisions of the Coleoidea. Zoologists recognize a primary division, based upon the number of arms, into the Decapoda and the Octopoda. Indeed Naef (1922) on embryological evidence regards the Octopoda as separating from the decapod line in the early Mesozoic, although fossil evidence does not indicate their presence prior to the Cretaceous. Coenogenetic modifications in the embryology might account for such an apparently fundamental difference without necessitating the hypothesis of such antiquity for the octopod line. The term Decapoda has several disadvantages. First, the same name has been used to embrace an order of the higher crustacea. Second, the value of the number of arms seems dubious. Recent finds, as yet unpublished, have lead the writer to conclude that the ten-armed condition may have been developed very early in orthoconic nautiloids and may even have been a primitive cephalopod feature. Further, all of the fossil "decapoda" do not possess 10 arms (Abel, 1916, p. 235–238), but some appear to have had as few as six. Therefore the system of Zittel (1885) and Hyatt (1900) of recognizing three major divisions, the Belemnoidea, the Sepioidea and the Octopoda, seems a better course, especially as it is in closer accord with the phylogeny.

The various classifications of the Coleoidea which have appeared since 1900 differ widely in the treatment of the Belemnoidea and Sepioidea, and it is impossible to summarize them properly in the present work. The views of Steinmann (1910), Pavlow (1913), Abel (1916), and Stolley (1919), have been considered and synthesized by von Bülow-Trummer (1920) who has made some valuable contributions of his own. This classification is notable for the fact that it is accompanied by succinct if not always satisfactory definitions of the generic and higher categories. Naef (1921, 1922) has developed a rather different scheme of classification, which presents some advantages but suffers from obscurity in the definition of higher groups, particularly in the belemnoids proper, and does not always explain clearly his reasons for rejecting the previously proposed classifications.

Von Bülow-Trummer (1920) divides the Phragmophori, which has the scope of the Belemnoidea of Zittel and Hyatt, into the sections Belemnoidea, Belemnoteuthidae and Spirulidae, groups which were families in earlier classifications. The Belemnoidea are divided into "tribes," the Protobelemnitidae and the Eubelemnitidae. The Protobelemnitidae are characterized by a very long dorsal proostracum and a short ventral proostracum, and embrace the family Aulacoceratidae. The Eubelemnitidae are characterized by the presence of "only a

very long dorsal proostracum" and embrace all other belemnoid families. These terms were proposed by Pavlow (1913). Stolley (1919) employed the Aulacoceratidae and Belemnitidae in the same way. Both classifications have the disadvantage of using "tribes" for groups embracing families instead of as divisions of families, and further of applying names to them with the suffix -idae, properly reserved for groups of family rank. To avoid such confusion as is presented by these terms, these groups will be referred to here as the aulacoceroids and the belemnoids.

Naef (1922) recognizes the Aulacoceratidae with essentially the scope given that family by Stolley and von Bülow-Trummer, except that *Xiphoteuthis* Huxley is removed to a new family. He does not, however, employ a dichotomous division of the belemnoids. Instead, he regards the Aulacoceratidae as a family equal in rank to many others. In his diagram of the phylogeny of the Coleoidea, however, he does give to this family an isolated position, and derives higher types, with doubt, from the primitive radicle of the Aulacoceratidae. Unfortunately, Naef fails to define the Aulacoceratidae clearly.

A search of the literature has, indeed, proved particularly fruitless in regard to any clear definition of the family. It would appear that the aulacoceroids have been recognized in general on the basis of a very slender phragmocone and widely spaced septa. The rostrum is generally long in these forms, sometimes digitiform, sometimes faintly clavate, but always long, extending far apicad of the tip of the phragmocone. However, a survey of the species, particularly those which have been placed in *Atractites*, indicates that the form of the phragmocone and the spacing of the septa vary widely, and several species have been described which approach so close to the general pattern of the higher belemnoids that it is difficult to see why they were included in the Aulacoceratidae at all. It is to be feared that the Triassic age of such species and the generally accepted concept that only Aulacoceratidae appeared in the Triassic are more responsible for this treatment than any morphological data.

The proostracal characters employed by von Bülow-Trummer in distinguishing the Protobelemnitidae from the Eubelemnitidae should find their greatest usefulness in distinguishing the smooth-shelled "Atractites" from belemnoids proper. Unfortunately there are some difficulties in either the use or the acceptance of this concept. Practical difficulties are encountered because proostraca are almost unknown in the Aulacoceratidae. Their presence can be inferred from conothecal striae. Indeed, this proposal was based primarily on the basis of the study of such striae. However, specimens which show even the conothecal striae are rare, particularly in the Triassic. The character is one which can be applied only to exceptionally well preserved specimens and cannot be used on typical material.

However, there is reason to question how thorough the investigation has been which leads to the separation of the Protobelemnitidae from the Eubelemnitidae. The conothecal striae have been figured for enough of the Eubelemnitidae to indicate that the inference that the same condition probably persists throughout the group is a fairly safe one. However the conothecal striae have not been adequately figured for the Aulacoceratidae. It seems unnecessary to reject the view that conothecal striae indicating a short ventral proostracum in addition to the long dorsal one exist in the

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EXPLANATION OF PLATE 65

FIGS. *1–6—Eobelemnites caneyense* Flower, n. sp. Holotype, U. S. National Museum. Mississippian boulder from the Johns Valley (Caney) shale of Oklahoma. *1*, Enlargement of ventral surface: Adapical portion sectioned, showing siphuncle; adoral portion shows various shell layers, with fine longitudinal lines on the conothecal surface; about ×2½. *2*, Portion of dorsal surface, ×2½, natural color, showing conothecal striae, dorsal ridge, and portion of the lateral asymptotes. *3*, Complete specimen, ×1, showing faint conothecal striae adapically, and rostrum. *4*, Phragmocone, lateral aspect, slightly reduced. *5*, Phragmocone ventral aspect, slightly reduced. *6*, Complete specimen, slightly reduced, unwhitened, showing polished surface of conotheca, traces of shell material, texture and structure of rostrum. (p. 492)

Flower, Mississippian Belemnite

family. However that the observations leading to the conclusion were not thorough is shown by the fact that no such condition exists in *Xiphoteuthis* Huxley, the proostracum of which is known. Yet von Bülow-Trummer not only included this in the Aulacoceratidae but regarded it as a synonym of the genus *Atractites*. *Xiphoteuthis* was removed from the Aulacoceratidae by Naef (1922) and was made the basis for a new family. However, Naef does not indicate that this was done on the basis of the proostracal features, which he dismisses perhaps too summarily.

Abel (1916) has brought another feature to bear upon the classification of the Belemnoidea, and one employed with modifications by later workers. He noted that embryonic rostra were present, and recognized two types, a clavirostrate condition, with a club-shaped rostrum apicad of the protoconch, and a conirostrate condition, in which he recognized a thin conical rostrum about the conotheca. Abel's conirostrate types are in general now regarded as forms lacking a true embryonic rostrum, and include the older and more generalized of the belemnoids. However, as might be expected, some relatively late survivals retain the condition while developing some characteristic specializations of their own, as in the case of the Belemnoteuthidae. However, Abel was mistaken in recognizing in *Aulacoceras* itself a clavirostrate condition, as shown by Naef (1922, p. 262–264). The matter is chiefly significant in that the appearance of the rostrum in the embryonal stages as a clavirostrate structure is evidently the result of tachygenesis, and is confined to the more specialized of the true belemnoids. Further, the embryonic rostrum seems to become larger in the younger and more specialized of these types. This is of interest in that it shows that the appearance of the rostrum as an embryonic feature is essentially tachygenetic, and appears long after the rostrum made its appearances in post-embryonic stages. Further, the tachygenetic series appears to be progressive, the most pronounced of the embryonic rostra appearing on the younger of the Belemnitidae. Were the series a proterogenetic one, the embryonic rostrum should be found in the earliest of the belemnoids.

Intricacies of the classification of the higher belemnoids are not of direct concern to the present problem, which deals with the relationship of *Eobelemnites* to the other Belemnoidea. It will suffice to point out that the classification of the later forms is primarily concerned with details of the ridges and grooves on the surface of the rostrum. Unfortunately, it is difficult to determine the precise relationship of *Eobelemnites*, mainly because of difficulties in ascertaining which of the several classifications mentioned above should be accepted. Assuming the correctness of the proostracal features employed to characterize the Protobelemnitidae, *Eobelemnites* should belong to this group. It differs from typical aulacoceroids, however, in the rapid expansion of the conotheca and in the closely spaced septa. A few species described in terms of the genus *Atractites* approach the condition of *Eobelemnites*, but none are closely similar in general proportions.

In the rapidly expanding conotheca and the closely spaced septa, *Eobelemnites* is closer to some of the Eubelemnitidae. But these forms differ from *Eobelemnites* in the arrangement of the conothecal striae on the ventral side of the shell. To a person not familiar with the actual material, *Eobelemnites* may appear to be very similar in general aspect to some of the Jurassic and more particularly Liassic species with which it was compared in the discussion accompanying its description. It is atypical in one other important feature, namely, the extremely well calcified condition of both the conotheca and the septa. The illustrated sections of Jurassic Belemnitidae give no true concept of the extreme fragility of the septa. Exposed and unflattened phragmocones are of rare occurrence in the Lias and younger deposits. Indeed, most Jurassic Belemnitidae reveal the septa only as the thinnest and most fragile structures. It is impossible to determine from the literature precisely how far actual phragmocones persist in the belemnoids. Certainly a point is finally reached at which the free part of the septum ceases to exist as a preservable structure, and the phragmocone can be recognized only by the annulated appearance of the cavity of the alveolus. This annulated appearance is due to the retention

of the mural part of the septa, and persists even into the Tertiary forms such as *Belosepia*.

In view of the uncertainties presented by the various and conflicting classifications it seems wisest not to attempt to refer *Eobelemnites* to any family at the present time. It combines the proostracal features of the aulacoceroids with an apical angle and a spacing of the septa more suggestive of the belemnoids. It is possible that it may represent a form ancestral to these stocks prior to their differentiation.

CONCLUSIONS

Eobelemnites caneyense is so preserved as to permit a close analysis of the structure of the phragmocone and conotheca. In the discussion of this form many features, first recognized in nautiloid shells, are reported for the first time among the belemnoids. However, these nautiloid features occur also in much younger and more specialized belemnoids, and indeed can be recognized on the basis of extant descriptions and illustrations.

The discovery of this form in apparently Mississippian boulders in the Caney shale indicates that the origin of the Coleoidea must be sought much earlier in the Paleozoic than was previously suspected. This form is already highly specialized, possessing proostracal and rostral features not markedly more primitive than those exhibited by some Mesozoic forms.

An attempt to determine the relationship of *Eobelemnites* in relation to the belemnoids previously described has not been very successful, largely because of difficulty in evaluating the several different concepts of classification and development, but also in part due to doubt as to the correctness of the morphological features by which major divisions among the Belemnoidea have sometimes been recognized. In the pattern of the conothecal striae *Eobelemnites* agrees with the Aulacoceratidae as defined by Stolley (1919) and von Bülow-Trummer. In the expansion of the conotheca and the spacing of the septa it suggests instead the higher belemnoids, the Eubelemnitidae of Pavlow and von Bülow-Trummer. Yet it is more primitive than known Eubelemnitidae in the strong calcification of the phragmocone, though the condition is perhaps approached by some Liassic genera which can, however, be differentiated by the absence of a ventral crest in the conothecal striae. These features suggest that *Eobelemnites* may represent the point of divergence of the aulacoceroids from the belemnoids. There are two possible objections to this view which may or may not disappear with further investigation. The first is uncertainty as to the validity of the conothecal striae as a criterion, on the basis that they have apparently been observed only very rarely in the aulacoceroids. The second is the previous failure to recognize any of the belemnoids in contrast to the aulacoceroids prior to the Upper Trias. However, the specialized condition of the Belemnoteuthidae as represented by *Phragmoteuthis*, the recognition of sepioids in the Muschelkalk, and the demonstration of the appearance of the Diploconidae as represented by *Metabelemnites* in the Upper Triassic of America, indicate that divergence of various stocks must have begun much earlier than the periods in which the first remains of these various subdivisions occur in abundance.

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JOURNAL OF PALEONTOLOGY, VOL. 19, NO. 5, PP. 504–521, PLS. 66, 67, 3 TEXT FIGS., SEPTEMBER 1945

GEOLOGIC APPLICATION OF BIOMETRICAL ANALYSIS OF MOLLUSCAN ASSEMBLAGES

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ABSTRACT—For any sample collection of eastern Pacific Recent mollusks, the median of midpoints is the latitude at which theoretically the total southward range of species would balance the total northward range. Calculation of the median is explained; and the results of new analyses are shown in a graph. This median of midpoint technique is applied to assemblages of late Cenozoic mollusks. Such analyses, in turn, are applied to the Pleistocene series of southern California, where the Lomita formation is treated as "upper Pliocene" and the Timms Point formation as "lower Pleistocene." A survey shows that although the technique is valid, additional carefully collected specimens, more ecological data, and taxonomic revisions are needed for more precise applications.

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INTRODUCTION

THIS was to have been a joint paper with A. Myra Keen, but because the pressure of her other work came at an inconvenient time for total collaboration, and because the writer is forced by circumstances to terminate this study now, it was decided to issue this report under the name of only one author. Paul Bartsch and Harold A. Rehder, United States National Museum, supplied most of the photographs of specimens illustrated in the accompanying plates. Robert C. Miller, G. Dallas Hanna, and Leo G. Hertlein donated information and loaned specimens. An especially fine collection of mollusks from the Lomita formation of Hilltop Quarry, California, was given to Stanford University by Rodman K. Cross. A score of active collectors whose recent work has directly benefited this paper might be named. In particular, thanks are due Rolf Bolin, E. P. and E. M. Chace, T. D. A. Cockerell, Charlotte L. Doty, Mackenzie Gordon, Jr., W. G. Hewatt, A. Sorensen, and George Willett. The exceptionally helpful contributions of S. S. Berry, John Q. and Thomas Burch, and W. H. Holman are much appreciated. For help in placing the paper in its present form the writer is indebted to Eliot Blackwelder and W. Egbert Schenck.

The sequence of general topics in this paper is this: (1) The method of biometrical analysis of molluscan assemblages is explained; (2) the results thus obtained are tested by further analyses; (3) since the results of analyses of Recent assemblages are consistent, the method is applied to stratigraphy; and (4) further data required for more precise applications of the technique are cited.

The method of analysis is simple. The midpoint of range of each species in the eastern North Pacific Ocean can be expressed in terms of latitude. Thus, if a species ranges from the equator to the North Pole, the midpoint, or center, of range of that species would be latitude 45° north. For a collection

of several species, one obtains a median of midpoints, or a "position average" which is not influenced by extreme variants to the same extent as is the mean. Hence, for a given collection of Recent mollusks from a certain locality, the median of midpoints is the latitude at which the total northward range of all the species would theoretically balance the total southward range.

The procedure followed in the calculation of the median likewise is simple. Given a number of shells from a locality, the worker identifies and names the species. Next, he prepares a list of the species, giving after each name the midpoint of range obtained from the compilation by Keen (1937), modified according to such data as he may have in addition. The accompanying tables illustrate this step. Third, he tallies the midpoints of the entire list of species. He determines, first approximately and then later, if necessary, by interpolation, the exact point on the latitude scale at which the median of midpoints falls.

For this report, the results of the calculations of the medians of midpoints of 34 collections of Recent mollusks were plotted on graph paper (text fig. 1). The purpose of this graph is to demonstrate that the medians do not perfectly correspond with the latitudes of the collections but that they deviate consistently.

Calculations of the medians of some collections that were obtained after the graph was first prepared confirm the general accuracy of the original data. Further tests were made by having university students identify specimens from localities unknown to them, and then requiring them to determine the collecting stations by the median method. It was found that students could determine the provenance to within about 2° of latitude, depending upon the size of the collection.

The consistency of results suggests that the method may be used in the comparison of late Cenozoic collections of mollusks. Early Pleistocene assemblages in southern California have medians of about 41° to 43°, whereas late Pleistocene ones range from about 32° to 36°, showing that the early assemblages lived in colder waters than the later. This conclusion is consonant with that of other workers, since the concept of shifts of water temperatures during the Cenozoic period is not new. The present method of analysis is an attempt to devise a fine-scale measure of these shifts.

This attempt necessitates a time-stratigraphic classification of late Pliocene and Pleistocene strata in southern California. A provisional scheme based on temperature shifts is proposed here. The Lomita is among the formations placed in the "upper Pliocene" stage. The Timms Point formation and synchronous strata which were deposited in a colder sea than those of late Pliocene, Pleistocene, and Recent times in southern California are included in the "lower Pleistocene" stage. The Palos Verdes and other strata are grouped into the "upper Pleistocene" stage. This classification appears to integrate with a scale calibrated in terms of medians of midpoints of collections of fossil mollusks.

Although this technique of measurement has potential utility in stratigraphy, it has limitations. Many more collections, accompanied by many stratigraphic and ecologic data, and numerous taxonomic revisions are needed in order further to exploit the index method.

CALCULATION OF MEDIAN

Mollusks from Shelter Cove, California

Table 1 is a list of specimens of 59 species collected at low tide at Shelter Cove, Cali-

TABLE 1.—MOLLUSKS FROM SHELTER COVE, CALIFORNIA

LATITUDE 40° 02′ N.,
Collected and identified by A. Myra Keen, 1935

Pelecypods	Range[1]	Midpoint
Clinocardium fucanum (Dall)	37–57	47
Clinocardium nuttallii (Conrad)	33–60	46
Entodesma saxicola (Baird)	30–54	42
Glans carpenteri (Lamy)	32–54	43
Kellia laperousii (Deshayes)	30–60	45
Macoma irus (Hanley)	37–64	50
Mytilus californianus Conrad	18–54	36
Mytilus trossulus Gould	34–48	42
Petricola carditoides (Conrad)	25–49	37
Pholadidea ovoidea (Gould)	23–60	41
Pholadidea penita (Conrad)	33–56	44
Protothaca staminea (Conrad)	23–73	48
Saxicava arctica (Linné)	8–72	40

[1] Range means the limits of distribution in terms of degrees of latitude for the eastern North Pacific Ocean.

TABLE 1.—*Continued*

Pelecypods	Range	Midpoint
Saxicava pholadis (Linné)	8–72	40
Schizothaerus capax (Gould)	37–58	47
Transennella tantilla (Gould)	27–57	42
Volsella modiolus (Linné)	27–72	49
Gastropods	**Range**	**Midpoint**
Acmaea asmi (Middendorff)	30–55	42
Acmaea digitalis Eschscholtz	19–55	37
Acmaea insessa (Hinds)	25–57	41
Acmaea instabilis (Gould)	37–51	44
Acmaea limatula Carpenter	21–48	34
Acmaea mitra Eschscholtz	34–56	45
Acmaea pelta Eschscholtz	19–60	39
Acmaea persona Eschscholtz	37–55	46
Acmaea scabra (Gould)	23–48	35
Acmaea scutum Eschscholtz	34–56	45
Amphissa columbiana Dall	34–56	45
Barleeia haliotiphila Carpenter	30–41	35
Bittium eschrichtii montereyense Bartsch	23–43	33
Calliostoma costatum (Martyn)	33–57	45
Crepidula adunca Sowerby	23–48	35
Crepidula nummaria Gould	16–65	36
Diodora aspera (Eschscholtz)	24–60	42

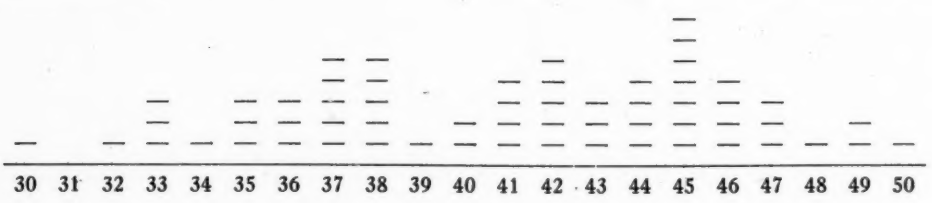
TABLE 1.—*Continued*

Gastropods	Range	Midpoint
Epitonium (Nitidiscala) tinctum (Carpenter)	23–49	36
Haliotis rufescens Swainson	23–42	32
Hipponix cranioides Carpenter	34–48	41
Homalopoma carpenteri (Pilsbry)	30–57	43
Lacuna marmorata Dall	33–57	45
Lacuna variegata Carpenter	34–48	41
Littorina planaxis (Philippi)	19–48	33
Littorina scutulata Gould	19–58	38
Margarites pupillus (Gould)	34–60	46
Mitrella gausapata (Gould)	27–60	43
Olivella biplicata (Sowerby)	25–49	37
Opalia chacei Strong	34–43	38
Pseudomelatoma torosa (Carpenter)	27–40	33
Purpura foliata Martyn	33–57	45
Schizopyga fossata (Gould)	27–49	38
Searlesia dira (Reeve)	37–56	46
Tegula brunnea (Philippi)	34–42	38
Tegula brunnea fluctuosa Dall	34–40	37
Tegula funebralis (A. Adams)	28–48	38
Thais emarginata (Deshayes)	16–58	37
Thais lamellosa (Gmelin)	34–65	49
Thais lima (Martyn)	28–66	47
Tritonalia circumtexta (Stearns)	19–42	30
Tritonalia interfossa (Carpenter)	32–56	44
Tritonalia lurida (Middendorff)	34–55	44

fornia, latitude 40°02′ north. The median of midpoints for this assemblage is computed in the following manner:

(1) Midpoints are found by reference to the summary of ranges given in Keen's (1937) abridged check-list.

(2) These numerical expressions of middle-of-range for each species are distributed along a horizontal scale, tallying each over its latitude, thus:



(3) Since the median is the exact latitude at which the middle species falls, divide the number of species in the list ($N=59$) by two yielding, in this instance, 29.5.

(4) Determine by inspection, that is, by counting up from the lower or left end of the distribution, the interval of latitude containing the middle species—in this distribution, the 42° interval, i.e., from 42°0′ to 42°59′. Interpolate to find the precise latitude of the median as follows:

(a) Count the number of tallies below (to the left of) this interval: in the above distribution, 29 species fall below 42°.

(b) Subtract this last result from $N/2$. $(29.5-29=0.5)$

(c) Divide the result of step b by the number of tallies in the median interval and multiply by the scale unit (in this example the unit of measurement is 1° of latitude):

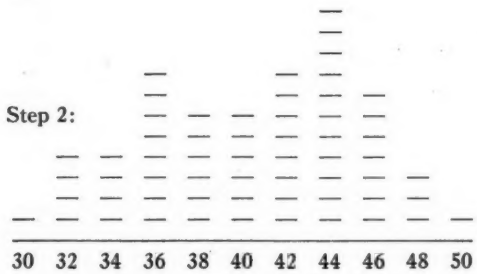
$$\frac{0.5\times 1^\circ}{5}=0.1^\circ$$

(d) Add this quantity to the lower limit of the median interval, thus obtaining the re-

quired median of midpoints:

$$42.0° + 0.1° = 42.1°$$

For distributions with a considerable spread of midpoints it is more convenient to group the tallies by using a unit interval of 2° of latitude. The computation for this same list (Shelter Cove) with a 2° class interval would be:



Step 3: $N=59$; $N/2=29.5$
Step 4a: 29 tallies below 42.0
Step 4b: $29.5-29.0=0.5$
Step 4c: $\frac{0.5}{8}\times 2°=0.125=0.1$
Step 4d: $42.0+0.1=42.1°$, the median.

Experience with calculations points to the desirability of having from about 15 to 25 classes. With less than 15, the accuracy of calculations decreases because of the coarseness of grouping. More than 25 necessitates the use of an unwieldy scale for tallying.

Mollusks off Redondo Beach, California

Table 2 is a list of mollusks dredged by John Q. and Thomas A. Burch in 50 to 150 fathoms off Redondo Beach, California, latitude 33°50′ ±. The temperature for the bottom samples was recorded as ranging from 49° to 57° Fahrenheit (1.5–14° C.) inclusive, or "cool temperate" as marine temperatures frequently are classified. By following the statistical procedure just explained, one computes the median for this assemblage to be 35.2°.

Mollusks Southeast of Farallon Islands

Table 3 is a list of 27 species published by Packard (1918) for the "most productive station" off Golden Gate in 33–46 fathoms, latitude 37°39′. The temperature range recorded at the nearest station was 9.4°–11.4°C. (48.9°–52.5°F.) The nomenclature

TABLE 2.—MOLLUSKS FROM 50–150 FATHOMS OFF REDONDO BEACH, CALIFORNIA

Collected and identified by John Q. and Thomas A. Burch, 1942

Pelecypods	Range	Midpoint
Acila castrensis (Hinds)	33–64	48
Aligena redondoensis Burch	33–34	33
Axinopsis viridis Dall	32–72	52
Compsomyax subdiaphana (Carpenter)	34–56	45
Crenella columbiana Dall	33–55	44
Cryptomya californica (Conrad)	11–59	35
Cuspidaria beringensis (Leche)	8–58	33
Cuspidaria californica Dall	33–48	40
Cuspidaria planetica Dall	32–60	46
Cyclopecten catalinense (Willett)[1]		34
Delectopecten randolphi (Dall)[1]	23–59	41
Delectopecten vancouverense (Whiteaves)[1]	33–58	45
Entodesma inflatum (Conrad)	−2–55	27
Lucina annulata (Reeve)	32–58	45
Macoma carlottensis Whiteaves	27–72	49
Macoma planiuscula Grant & Gale	48–72	60
Macoma quadrana Dall	32–55	43
Nemocardium centifilosum (Carpenter)	33–38	34
Nucula tenuis (Montagu)	32–73	52
Nuculana cellulita (Dall)	34–48	41
Nuculana hamata (Carpenter)	8–48	28
Nuculana lomaensis (Dall)	33–34	33
Nuculana oxia (Dall)	23–24	28
Pandora filosa (Carpenter)	34–60	47
Pecten diegensis Dall	28–37	32
Periploma discus Stearns	33–37	35
Poromya tenuiconcha Dall	32–57	44
Pseudochama granti Strong	34–37	35
Rochefortia aleutica (Dall)	32–60	46
Saxicava arctica (Linné)	8–72	40
Saxicavella pacifica Dall	33–37	35
Solemya johnsoni Dall	0–48	24
Solemya panamensis Dall	8–37	22
Tellina idae Dall		34
Tellina carpenteri Dall	8–55	31
Thracia trapezoides Conrad	36–56	46
Thyasira barbarensis Dall	23–48	35
Verticordia ornata d'Orbigny	8–36	22
Volsella pallidula (Dall)[2]	28–38	33
Yoldia scissurata Dall	48–72	60
Gastropods and Scaphopods		
Acmaea mitra Eschscholtz	34–56	45
Acteocina intermedia Willett		33
Admete gracilior Carpenter	33–71	52
Admete rhyssa Dall	32–34	33

[1] *Cyclopecten* Verrill, 1897, was considered by Willett a subgenus of *Pecten*. These "mud pectens" have shuttled from one genus to another. In Keen (1937, p. 24) they are recorded as *Pseudamusium*. Woodring (U. S. Geol. Survey Prof. Paper 190, pp. 35–42, 1938) considers them under the genus name *Hyalopecten*, recognizing *Delectopecten* as a subgenus.

[2] Listed as *Modiolus* by Keen (1937, p. 22).

TABLE 2.—*Continued*

Gastropods and Scaphopods	Range	Mid-point
Alvania pedroana Bartsch		34
Alvania rosana Bartsch		34
Amphissa bicolor Dall	33–38	35
Antiplanes perversa (Gabb)[3]	30–55	42
Antiplanes rotula Dall	33–55	44
Antiplanes santarosana Dall	33–36	34
Bittium asperum Gabb	27–34	30
Bittium catalinense Bartsch	33–34	33
Bittium interfossa Carpenter	27–37	32
Bittium subplanatum Bartsch	32–37	34
Borsonia bartschi (Arnold)[4]	33–34	33
Bursa californica (Hinds)	27–37	32
Cadulus californicus Pilsbry & Sharp	−1–56	27
Cadulus fusiformis Pilsbry & Sharp	23–37	30
Cadulus hepburni Dall	34–61	48
Cadulus stearnsii Pilsbry & Sharp	30–49	39
Cadulus tolmiei Dall	30–49	39
Calliostoma turbinum Dall	33–34	33
Calyptraea fastigiata Carpenter	48–56	52
Cancellaria crawfordiana Dall	33–38	35
Capulus californicus Dall	29–34	31
Cerithiopsis antemunda Bartsch	33–34	33
Cerithiopsis oxys Bartsch	27–34	30
Cidarina cidaris (A. Adams)	30–55	42
Clathurella cymodoce (Dall)[5]	34–37	35
Clavus empyrosia (Dall)[6]	33–34	33
Dentalium neohexagonum Sharp & Pilsbry	8–37	22
Dentalium numerosum Dall	−1–34	17
Dentalium rectius Carpenter	8–56	32
Dentalium vallicolens Raymond	23–48	35
Dentalium watsoni Sharp & Pilsbry	33–45	39
Engina strongi Pilsbry & Lowe	34	34
Epitonium acrostephanum Dall	33–48	40
Epitonium catalinae Dall	33–55	43
Epitonium cooperi Strong	23–49	36
Epitonium densiclathratum Dall	33–48	40
Epitonium sawinae Dall	34–38	41
Exilioidea recitrostris (Carpenter)	30–56	43
Forreria catalinensis (Oldroyd)[7]	34–35	34
Homalopoma paucicostatum (Dall)	30–36	43
"*Lora*" *kyskana* Dall	34–52	43
Mangelia crassaspera Grant & Gale	33–37	35

[3] *Spirotropis* Sars, 1878, has for its type *Pleurotoma carinata* Philippi, 1844, the original figure of which is reproduced by Tryon (Man. Conch. vol. 6, pl. 7, fig. 94). Grant and Gale (1931, p. 547) were clearly in error in taking Sars' later-published figure as "the type of the genus." The genotype is Philippi's *species*, not Sars' concept of the species nor his figure of a specimen. *Antiplanes* (genotype: *Pleurotoma perversa* Gabb) is here accepted as the correct generic allocation.

[4] Listed as *Borsonella* by Keen (1937, p. 31).

[5] Listed by Keen (1937) as *Glyphostoma*.

[6] Listed by Keen (1937) as *Cymatosyrinx*.

[7] Listed by Keen (1937) as *Trophon*.

TABLE 2.—*Continued*

Gastropods and Scaphopods	Range	Mid-point
Mangelia roperi Dall	23–37	30
Mangelia variegata Carpenter	23–37	30
Margarites pupillus (Gould)	34–60	46
Melanella catalinensis Bartsch	27–34	30
Melanella rutila Carpenter	25–55	40
Micranellum crebicinctum (Carpenter)	30–55	42
Microglyphis breviculus Dall	30–37	33
Mitra montereyensis Berry	33–37	35
Mitrella gouldi (Carpenter)	24–55	39
Murex petri Dall	33–37	35
Nassarius insculptus (Carpenter)	28–39	33
Natica salimba Dall	23–35	29
Neptunea tabulata (Baird)	33–51	42
Odostomia amianta Dall & Bartsch	27–37	32
Odostomia dinella Dall & Bartsch		34
Odostomia eugena Dall & Bartsch	27–34	30
Odostomia farallonensis Dall & Bartsch		38
Odostomia helena Bartsch		34
Odostomia io Dall & Bartsch	33–34	33
Odostomia talpa Dall & Bartsch	48–60	54
Odostomia trachis Dall & Bartsch	33–37	35
Odostomia valdezi Dall & Bartsch	32–58	40
Philbertia crystallina (Gabb)		34
Polinices acosmitus Dall		34
Polinices draconis (Dall)		45
Polinices pallidus (Broderip & Sowerby)	34–72	53
Puncturella cucullata Gould	23–58	40
Puncturella galeata Gould	34–54	44
Simnia barbarensis Dall	23–37	30
Sinum scopulosum (Conrad)	32–37	34
Solariella peramabilis Carpenter	32–55	43
Strombiformis californicus Bartsch	33–34	33
Tachyrhynchus pratomus Dall	23–56	40
Taranis strongi Arnold	33–55	44
Tritonalia painei Dall	33–55	44
Trophon bentleyi Dall	33–34	33
Trophon orpheus Gould	34–48	41
Trophon lasius Dall	32–60	46
Turbonilla aresta Dall & Bartsch	33–34	33
Turbonilla chocolata Carpenter	33–34	33
Turbonilla mörchi Dall & Bartsch	33–34	33
Turbonilla profundicola Dall & Bartsch	33–34	33
Turbonilla regina Dall & Bartsch		34
Turbonilla stylina Carpenter	33–37	35
Turbonilla torquata Gould	33–34	33
Turbonilla weldi Dall & Bartsch		34
Turritella cooperi Carpenter	28–37	32
Verticumbo charybdis Berry		34
Volvulella californica Dall		33
Volvulella cooperi Dall	28–37	32
Volvulella cylindrica (Carpenter)	23–48	35

N = 139
Latitude = 33° 50′
Median = 35.2

given by Packard has been somewhat revised by A. M. Keen. Following the procedure outlined previously one calculates

the median of midpoints for this collection to be 41.7°.

TABLE 3.—MOLLUSKS COLLECTED BY U. S. BUREAU OF FISHERIES STEAMER "ALBATROSS," 1912–13, AT STATION 5789, SOUTHEAST OF FARALLON ISLANDS, 33–46 FATHOMS

Identified by Earl L. Packard, nomenclature modernized by A. M. Keen

Pelecypods	Range	Midpoint
Acila castrensis (Hinds)	32–64	48
Compsomyax subdiaphana (Carpenter)	34–56	45
Cuspidaria californica Dall	33–48	40
Lucinoma annulata (Reeve)	32–58	45
Macoma yoldiformis (Carpenter)	33–49	41
Mytilus edulis Linné	28–74	51
Nemocardium centifilosum (Carpenter)	30–38	34
Nuculana hamata (Carpenter)	8–48	28
Nuculana taphria (Dall)	30–38	34
Pandora filosa (Carpenter)	34–60	47
Parvilucina tenuisculpta (Carpenter)	32–50	46
Volsella pallidula (Dall)	28–38	33
Yoldia ensifera Dall	36–56	46
Gastropods and Scaphopods		
Acteocina culcitella (Gould)	33–58	45
Acteon punctocaelatus (Carpenter)	23–55	39
Cadulus fusiformis Pilsbry & Sharp	23–37	30
Cancellaria crawfordiana Dall	33–38	35
Dentalium pretiosum Sowerby	33–55	44
Epitonium sawinae Dall	34–49	41
Magnelia barbarensis I. Oldroyd	23–48	35
Megasurcula carpenteriana (Gabb)	32–38	35
Melanella micans (Carpenter)	27–60	43
Mitrella gausapata (Gould)	27–60	43
Nassarius perpinguis (Hinds)	28–48	38
Neptunea tabulata (Baird)	33–51	42
Polinices draconis (Dall)	32–58	45
Volvulella cylindrica (Carpenter)	23–48	35

N = 27
Latitude = 37° 39′ North.
Median = 41.7°

Mollusks from Mayne Island, British Columbia

Table 4 is based upon specimens of 28 species collected by the writer at low tide on Mayne Island, 48°50′, British Columbia, Canada. The calculated median is 45.5°.

RESULTS OF ANALYSES

Figure 1 shows the relations between the medians of midpoints for 29 shore collections and five shallow dredgings from the eastern North Pacific Ocean. The latitude of each collection locality is given on the left. The median of midpoints for each assemblage is shown by the circle plotted over the computed latitude. For example, the median of the Shelter Cove collection (table 1) is shown by the circle over latitude 42.1° on the horizontal coordinate and to the right of latitude 40.2° on the vertical coordinate. All medians would fall along the straight diagonal line extending from the lower left to the upper right of the figure if there were a perfect correspondence between the latitude of the collection locality and the median of midpoints of range. The consistent deviations from this correspondence are obvious. One may infer that the same factors which underlie the formation of zoölogical provinces are in operation here for shore collections.

This graph is an improved version of one

TABLE 4.—MOLLUSKS COLLECTED BY HUBERT G. SCHENCK, 1941, ON MAYNE ISLAND, BRITISH COLUMBIA

Identifications by D. A. Myers

Pelecypods	Range	Midpoint
Clinocardium nuttallii (Conrad)	33–60	46
Hinnites multirugosus Gale	25–54	39
Macoma incongrua (Martens)	33–72	52
Macoma irus (Deshayes)	37–64	50
Macoma nasuta (Conrad)	28–60	44
Mya arenaria (Linné)	37–49	43
Mytilus edulis Linné	28–74	51
Mytilus edulis cf. *trossulus* (Gould)	37–48	42
Pododesmus macroschismus (Deshayes)	30–57	43
Protothaca staminea (Conrad)	23–73	48
Saxidomus giganteus (Deshayes)	37–56	46
Schizothaerus capax (Gould)	37–58	47
Solen sicarius (Gould)	30–49	39
Volsella flabellata (Gould)[1]	33–49	41
Volsella modiolus (Linné)[1]	27–72	49
Gastropods		
Acmaea digitalis Eschscholtz	19–55	37
Acmaea mitra Eschscholtz	34–56	45
Acmaea pelta Eschscholtz	19–60	39
Acmaea persona Eschscholtz	37–55	46
Acmaea scutum Eschscholtz	34–56	45
Bittium eschrichtii (Middendorff)	48–57	52
Crepidula nummaria Gould	16–65	41
Diodora aspera (Eschscholtz)	24–60	42
Littorina scutulata (Gould)	19–58	38
Littorina sitkana (Philippi)	48–56	52
Polinices lewisii (Gould)	33–51	42
Searlesia dira (Reeve)	37–56	46
Thais lamellosa (Gmelin)	34–65	49

N = 28
Latitude = 48° 50′
Median = 45.5°
[1] Listed as *Modiolus* in Keen (1937, p. 22).

previously published (Schenck and Keen, 1937, fig. 2). The major alteration here, aside from differences in mode of drafting, is that certain medians have been recalculated. Subsequent experience has shown that samples should preferably comprise at least 50 species; a smaller number may result in a sampling error of as much as 2° of latitude. Therefore, several previous medians which were based upon meager lists have been corrected here either by fresh collecting or by the combination of several lists from points within 30′ of latitude of the stated locality. Such are shown here as areas, as for example "Tillamook Bay area."

Additional confirmation of the validity of the medians was furnished recently by intensive collecting by Charlotte L. Doty at Coos Bay, Oregon. A collection of 54 gastropod species, 44 of which had not been reported in this area in previous lists, yielded a median of 43.1°, as compared to a median of 44.0° for the pelecypod fauna of the bay itself. Still further confirmation comes from an analysis of the species from off Redondo Beach as shown in table 2. The median of

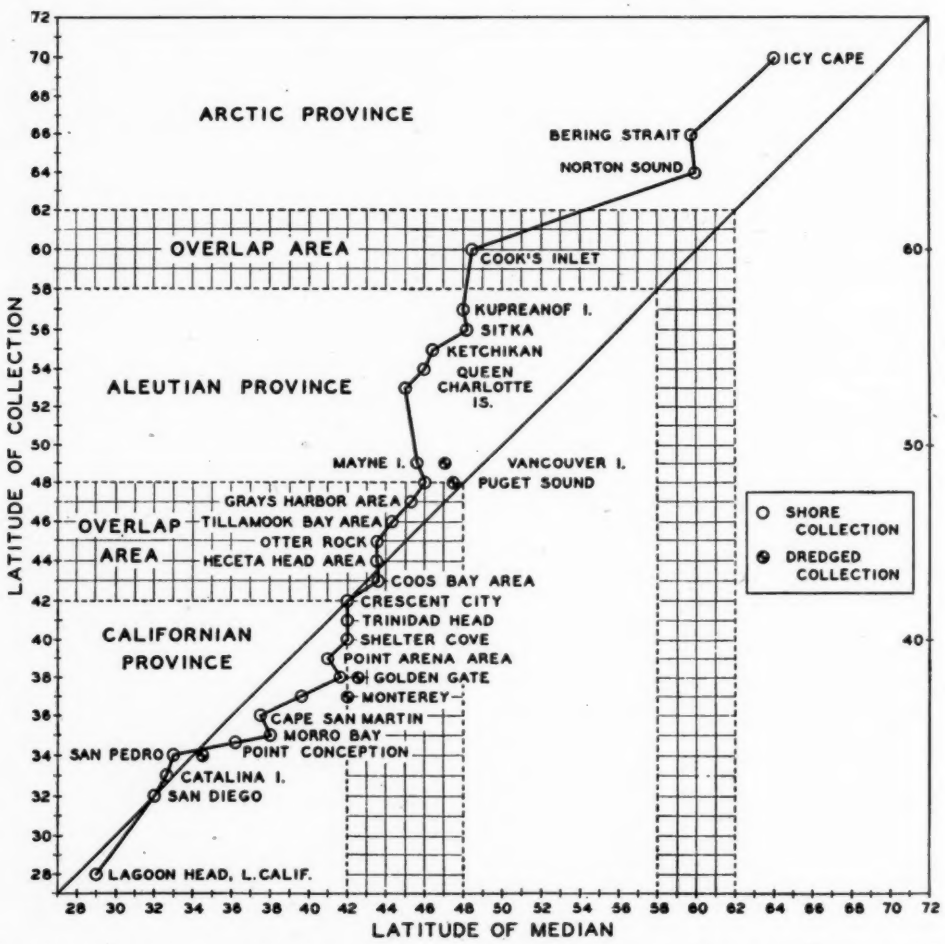


FIG. 1—Curve of medians of midpoints for sample West American Recent marine molluscan collections. Medians for shore collections are connected by unbroken line to show deviation from the norm, which is the heavy diagonal line. Provincial boundaries are superimposed for reference.

midpoints of 35.2° agrees so closely with the previous calculation that the new information was not added to figure 1. Noteworthy also is the list of gastropod species given by Vokes (1936) for intertidal material at Moss Beach, latitude 37°31′; the median for this assemblage is 39.3°.

The consistency of the calculations has been tested in two ways. First, new shore collections from localities intermediate to those of the initial study (Schenck and Keen, 1936, 1937) have been obtained and analyzed. Without exception, these fall at or near the points on the curve which would be predicted by inspection of the adjacent medians. For example, a collection of specimens of 95 species was made in 1939 by W. G. Hewatt on Santa Cruz Island (lat. 34°); this yields a median of 34.7°. The median for the assemblage taken on Mayne Island, British Columbia (table 4) is 45.5° as against 46° for the entire Puget Sound area. Second, senior students in geology have repeatedly been given sample shore collections of less than 30 specimens with unrevealed localities. Previous experience had proved that one could expect that the analysis of each collection would indicate the locality within 2° of latitude. The students were instructed to identify the specimens and to compute the medians of such assemblages. These university undergraduates estimated the latitudes at which the collections were actually made, as expected.

Particular attention is invited to this fact: the median of midpoints for dredged collections (down to 150 fathoms) off southern California (table 2) is not as high as the median for intertidal collections in northern California. The median for dredgings off Redondo Beach approximates the median for intertidal collections on Santa Cruz Island; both are lower than the median for the shallow dredging (table 3) off Golden Gate and for the low-tide material (table 2) at Shelter Cove. Therefore, the bathymetric gradient so often mentioned in biogeographic discussions is real and measurable, but it is not of sufficient size to vitiate the use of range data.

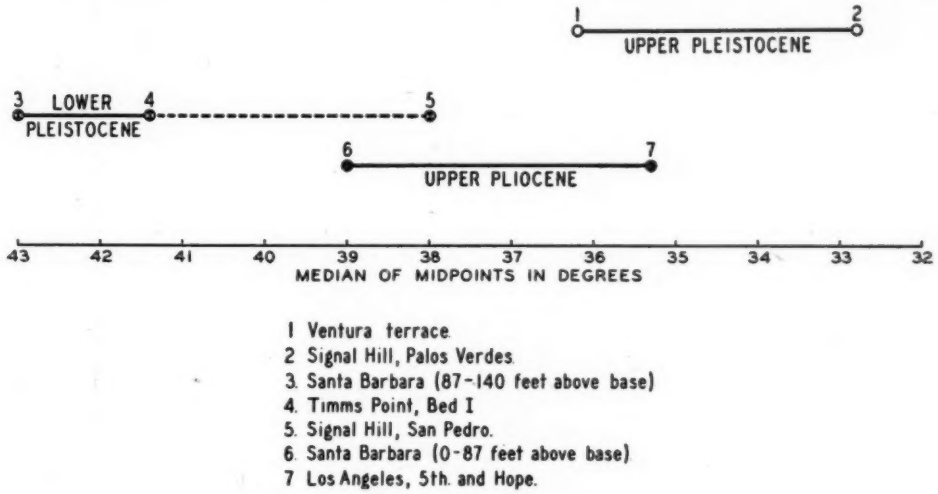


FIG. 2—Graphic presentation of data from table 6 to show the climatic-chronologic classification expressed on a median of midpoints scale.

USES OF METHOD

Western North America

The index method may be used with certain precautions as a rapid means of analyzing late Tertiary and Quaternary faunules. Pleistocene assemblages from the San Pedro area in California vary in medians between about 32° and 43° north latitude. The earlier Pleistocene mollusks have more northerly affinities than the later Pleistocene ones.

These findings are consonant with those of other workers, notably Ashley (1895), Arnold (1903), Smith (1919), and Grant (1936). Repeated testing by different methods has thus proved the validity of the general idea of shifts of water temperatures during late Cenozoic time. What the writer is attempting here is to devise a fine-scale measure for these shifts.

Since the medians for shore collections and dredgings down to 150 fathoms are consistent, the medians for assemblages of fossil mollusks from similar environments should be equally consistent. Hence, if the assemblage from bed 2 at Timms Point (latitude 34°) shows a median of midpoints of 42.7°, the inference is that one should look to the littoral zone of northern California or to deeper water off central California (such as that off Golden Gate) for living representatives of the same species as occur in the Pleistocene bed. The reason for this inference is that the localities from which similar medians today are obtained, as shown in figure 1, are on the shore of Cresent Bay and Coos Bay and in relatively shallow dredgings off San Francisco. The symbol for the dredged material labelled "Golden Gate" in figure 1 being at approximately 42.7° suggests that the molluscan community living at Timms Point during the time of deposition of bed 2 inhabited water having the same temperature (about 50°F.) as the sea floor off Golden Gate or the surface waters in the vicinity of Crescent City today. This, in brief, is an explanation of the application of the index method to the ecologic interpretation of fossil faunas.

The Lomita formation underlies the Timms Point formation. The molluscan fauna from the Lomita is listed in table 5. The median of the assemblage is 37°. This suggests sea temperatures comparable with those prevailing today along the coast between Monterey Bay and Cape San Martin, or in waters down to some 150 fathoms between Cape San Martin and Redondo Beach, where the temperature range is from about 50° to 58° Fahrenheit, questionably 62°F., as Grant (1936, p. 349) suggested.

The strata containing the assemblage from Hilltop Quarry and other late Cenozoic ones in southern California from Santa Barbara southward to the Los Angeles area may be grouped into a time-stratigraphic classification in which water temperature plays a critical role. The Pleistocene series is divided into two time-stratigraphic units

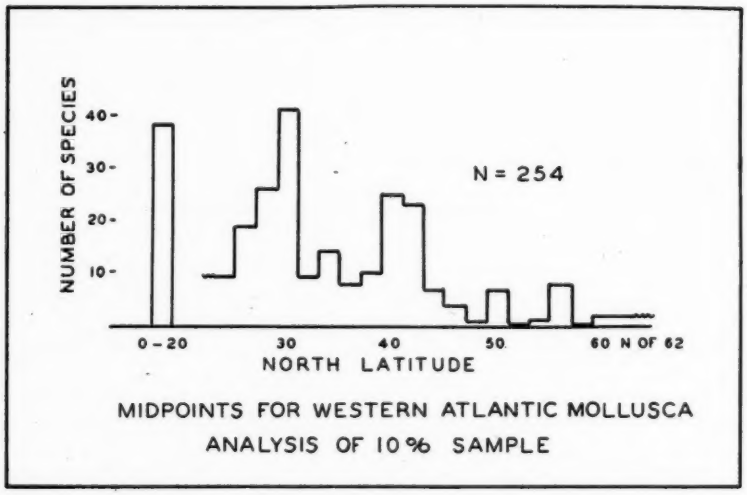


FIG. 3—Midpoints for western Atlantic mollusks computed for the species on every tenth page of the list by Johnson (1934).

TABLE 5.—MOLLUSKS FROM THE LOMITA FORMATION, "UPPER PLIOCENE," HILLTOP QUARRY, SAN PEDRO HILLS QUADRANGLE, CALIFORNIA

Specimens collected by S. S. Berry, E. P. Chace, and R. K. Cross; provisional identifications by S. S. Berry. Range and midpoint refer to living representatives of species.

Pelecypods	Range	Midpoint
Arca (*Arca*) *sisquocensis* Reinhart		
Cardita (*Miodontiscus*) *prolongata* (Carpenter)	33–59	46
Cardita cf. *ventricosa* Gould	32–55	43
Chlamys aff. *behringianus* (Middendorff)	56–66	61
Crassatella lomitensis (Oldroyd)		
Crenella divaricata d'Orbigny	8–37	22
Glans carpenteri (Lamy)	32–54	43
Glycymeris barbarensis (Conrad)		
Glycymeris subobsoleta (Carpenter)	48–56	52
Lucina (*Codakia*) *californica* Conrad	27–42	34
Lucina (*Parvilucina*) *tenuisculpta* Carpenter	32–60	46
Nemocardium centifilosum (Carpenter)	30–38	34
Nuculana praecursor (Arnold)		
Psephidia cymata Dall	23–34	28
Psephidia ovalis Dall	33–57	45
Pseudochama cf. *exogyra* (Conrad)	2–45	26
Saxicava arctica (Linnaeus)	8–72	40
Semele pulchra (Sowerby)	0–37	17
Tellina carpenteri Dall	8–55	31
Transennella tantilla (Gould)	27–57	42
Trachycardium quadragenarium (Conrad)	32–37	34
Ventricola fordii (Yates)	23–37	30
Gastropods and Scaphopods		
Acmaea lepisma Berry		
Actaeon (*Microglyphis*) *schencki* Berry		
Admete gracilior Carpenter	33–71	52
Alabina californica (Dall & Bartsch)		34
"*Alabina*" *effiae* Willett		
Aletes squamigerus (Carpenter)	−1–55	27
Alvania acutilirata (Carpenter)	30–37	33
Antiplanes perversa (Gabb)	30–55	42
Astraea (*Pachypoma*) *inaequalis montereyensis* Oldroyd		37
Astraea (*Pomaulax*) *petrohauma* Berry		
Astraea (*Pomaulax*) *undosa* (Wood)	26–34	30
Balcis (*Vitreolina*) *thersites* (Carpenter)[1]	30–37	33
Barleeia marmorea (Carpenter)	34–54	44
Barleeia oldroydi Bartsch	33–49	41
Bittium asperum (Gabb)	27–34	30
Bittium attenuatum Carpenter	30–55	42
Bittium catalinense Bartsch	33–34	33
Bittium rugatum Carpenter	32–34	33

[1] Listed as *Melanella* by Keen (1937, p. 40).

TABLE 5.—*Continued*

Gastropods and Scaphopods	Range	Midpoint
Boreotrophon triangulatus (Carpenter)	33–34	33
Bursa californica (Hinds)	28–37	32
Caecum (*Micranellum*) *crebicinctum* Carpenter	30–55	42
Calliostoma canaliculatum nebulosum Dall		33
Calliostoma grantianum Berry		
Calliostoma cf. *supragranosum* Carpenter	26–37	31
Calyptraea cf. *contorta* (Carpenter)	23–34	28
Cantharus fortis (Carpenter)		
Clathurella canfieldi Dall[2]	33–41	37
Clathurella conradiana (Gabb)		
Clathurella tridesmia Berry		
Clavus (*Crassispira*) *zizyphus* Berry		
Conus californicus Hinds	26–38	32
Crepidula adunca Sowerby	23–48	35
Crepidula lingulata Gould	8–60	34
Crepidula nummaria Gould	16–65	41
Cypraea fernandoensis Arnold		
Dentalium pretiosum Nuttall	33–55	44
Diodora murina (Dall)	21–42	31
Epitonium (*Opalia*) *chacei* Strong	34–43	38
Fusinus barbarensis (Trask)	33–44	38
Fusinus monksae Dall	26–50	38
Halistylus sub-pupoideus (Tryon)	8–55	31
Homalopoma bacula (Carpenter)	30–48	39
Homalopoma carpenteri (Pilsbry)	30–57	43
Homalopoma fenestratum (Bartsch)	32–36	34
Homalopoma paucicostatum (Dall)	30–36	33
Iselica fenestrata (Carpenter)	23–48	35
Kelletia kelletii Forbes	30–34	32
Liotia acuticostata bristolae Baker	32–33	32
Liotia fenestrata Carpenter	30–37	33
Macron aethiops Reeve		
Margarites (*Lirularia*) *arestus* Berry		
Margarites (*Lirularia*) *lirulatus* (Carpenter)	33–57	45
Margarites (*Lirularia*) *parcipictus pedroanus* (Arnold)		
Margarites cf. *pupillus* (Gould)	34–60	46
Marginella jewettii Carpenter	27–37	32
Marginella (*Cypraeolina*) *pyriformis* (Carpenter)	23–58	40
Marginella (*Cystiscus*) *regularis* Carpenter		
Mitra catalinae (Dall)	33–42	37
Mitrella luberosa (Carpenter)	23–55	39
Mitromorpha barbarensis woodfordi Berry		
Mitromorpha galeana Berry		
Moniliopsis chacei Berry		
"*Murex*" *eldridgei* Arnold		
"*Murex*" *gemma* Sowerby	27–34	30

[2] Listed as *Philbertia canfieldi* by Keen (1937, p. 44).

TABLE 5.—*Continued*

Gastropods and Scaphopods	Range	Mid-point
"Murex" santarosanus (Dall)	28–34	31
Nassarius fossatus (Gould)	27–49	38
Nassarius insculptus (Carpenter)	28–39	33
Nassarius (Schizopyga) mendicus cooperi (Forbes)	33–48	40
Nassarius (Schizopyga) perpinguis (Hinds)	38–48	38
Natica (Tectonatica) cf. *clausa* Broderip & Sowerby	?54–72	63
Neptunea tabulata (Baird)	33–51	42
Norrisia norrisii (Sowerby)	28–37	32
Ocinebra barbarensis (Gabb)[3]	34–49	41
Ocinebra lurida munda (Carpenter)	33–59	46
Ocinebra subangulata (Stearns)	34–38	36
Oenopota turrispira Berry		
Oenopota cf. *viridula* Fabricius		
Olivella baetica Carpenter	23–57	40
Olivella biplicata (Sowerby)	25–49	37
Phasianella compta Gould	23–37	30
Pseudomelatoma penicillata semiinflata Grant & Gale		
Puncturella cucullata (Gould)	23–58	40
Retusa harpa (Dall)	30–55	42
Rissoina kelseyi Dall & Bartsch	32–34	33
Skenea? cyclostoma Berry		
Taranis strongi (Arnold)	33–55	44
Tegula (Chlorostoma) aureolincta (Forbes)	23–34	29
Tegula (Chlorostoma) funebralis (Adams)	28–48	38
Turritella pedroensis Merriam		

N = 84, excluding species without range data
Latitude of collection = 33° 44′
Median = 37°

[3] Listed as *Tritonalia barbarensis* by Keen (1937, p. 47). All workers do not agree that Berry is correct is allocating this and other species to *Ocinebra* instead of to *Tritonalia*.

(see Schenck & Muller, 1941) called the "upper Pleistocene" and "lower Pleistocene" stages pending the proposal of proper local names and definitions. The stage below the "lower Pleistocene" is referred to as "upper Pliocene." The quotation marks are intended to indicate recognition of the difficulty of precisely applying European names to American stratigraphic divisions.

The letters A, B, C, D, E, and F before the names of the localities in table 6 refer to data supplied by W. H. Holman. These initials indicate the correct sequence of strata as determined by foraminiferal correlations. Thus, the letter B—San Pedro formation of Signal Hill—refers to strata which Holman believes are younger than bed 1 of the Timms Point formation, or C on the table. Holman points out (letter dated May 13, 1943) that the so-called Pico formation of 5th and Hope streets (E) in Los Angeles is younger than the Pico formation at its type locality. He also says that F (lower 87 feet of the type Santa Barbara formation) is nearly the same age as or slightly younger than E.

Superpositional control governs the general arrangement in table 6. That the Timms Point formation is stratigraphically above the Lomita formation has been mentioned. Further evidence of stratigraphic order has been advanced by Tieje (1926) who described in a continuous sequence immediately north of the Baldwin Hills: Timms Point equivalent, San Pedro, Palos Verdes, and Centinela gravels.

Correlations of strata in southern California led Grant (1936, p. 349–350) to adopt a four-fold classification. The sequence of marine formations which he recognized in order of increasing age is Palos Verdes, San Pedro, Timms Point, and Lomita. Perhaps this is the best of all possible arrangements. If the Lomita is excluded from the Pleistocene, that leaves three divisions for the Pleistocene—lower, middle, and upper Pleistocene. The adoption of this scheme would mean that the San Pedro formation of Signal Hill and other strata would become "Middle Pleistocene" in a stage classification. The question to be settled concerns the magnitude of the divisions of the Pleistocene series. The writer is inclined to the opinion that "lower" and "upper," rather than a threefold division, constitute time-stratigraphic divisions of the magnitude of other Cenozoic stages.

The important difference between table 6 and Grant's classification is that he treats the Lomita formation as a part of the Pleistocene series, whereas in this paper it is placed in the "upper Pliocene" stage. This is important because by the present arrangement the lower limit of the Pleistocene series in southern California is drawn at that horizon marked by beds containing a "cold-water" fauna. In other words, the Pleistocene epoch began with "glacial" conditions.

Some of the problems of the Pliocene and Pleistocene in California have been dis-

cussed by Eaton (1928, 1941), Grant and Hertlein (1941), and Wissler (1941). The reader of these articles will be convinced that a guiding principle is needed for establishing the Pliocene-Pleistocene boundary. Some readers may even welcome the arbitrary decision made here. It might be mentioned, in passing, that stratigraphic nomenclature is often confusing. If the Timms Point formation is considered to underlie the San Pedro, and if it is granted that the Timms Point is Pleistocene, then it follows that "lower Pleistocene" is not synonymous with "Pedroian" as used by Eaton (1928, p. 123).

TABLE 6.—PRELIMINARY STAGE CLASSIFICATION OF SOME LATE CENOZOIC FORMATIONS IN SOUTHERN CALIFORNIA WITH MEDIANS OF MIDPOINTS OF MOLLUSCAN FAUNAS

Stage	Locality	Latitude	Formation	Authority	Median
"Upper Pleistocene"	Ventura	34° 16′	Terrace	Putnam, 1942	36° 12′
	Point Loma	32° 40′	Terrace	Webb, 1937	35° 06′
	A. "Baldwin Hills"	34° 01′	Centinella gravels of Tieje (1926)	Willett, 1938	33° 24′
	Signal Hill	33° 48′	Palos Verdes	DeLong, 1941	32° 48′
——— ? ———	B. Signal Hill	33° 48′	San Pedro	DeLong, 1941	38°
——— ? ———					
"Lower Pleistocene"	C. San Pedro	33° 44′	Timms Point, Beds II & III.	A. Clark, 1931	42° 42′
	C. San Pedro	33° 44′	Timms Point, Bed I.	A. Clark, 1931	41° 24′
	Santa Barbara	34° 24′	Santa Barbara (87–140 feet above base)	Keen & Bentson (1944)	43°
"Upper Pliocene"	D. San Pedro (Hilltop Quarry)	33° 45′ 15″	Lomita	Berry (MS)	37°
	E. Los Angeles, 5th and Hope Sts.	34° 02′	"Pico"	Soper & Grant, 1932	35° 18′
	Los Angeles, 6th & Flower Sts.	34° 02′	"Pico"	Soper & Grant, 1932	35° 24′
	Los Angeles, 4th & Broadway Sts.	34° 02′	"Pico"	Soper & Grant, 1932	38° 54′
	F. Santa Barbara	34° 24′	Santa Barbara (0–87 feet above base)	Keen & Bentson (1944)	39°

The data in table 6 may be plotted on a median of midpoints scale, as in figure 2. The area covered by the figure is from Santa Barbara to the Los Angeles region. Accepting the assignment of the lower 87 feet of the Santa Barbara formation and the beds at 5th and Hope streets in Los Angeles to the "upper Pliocene," one may use the medians of these two assemblages as the terminals for the upper Pliocene line on the chart. Significantly enough, the medians of other "upper Pliocene" assemblages fall between these two terminals, as they should. The part of the Santa Barbara formation above a level 87 feet from the base is taken as "lower Pleistocene" and is point 3 on the chart; Timms Point formation, bed 1, is point 4; the full line connecting these terminals covers the range of midpoints for definite "lower Pleistocene" molluscan assemblages, in southern California. The dashed line to point 5 (San Pedro formation of Signal Hill) shows that if this assemblage is also considered "lower Pleistocene" rather than "middle" the spread is considerably greater and the overlap with the "upper Pliocene" is evident. The medians for the collection from the Ventura terrace, point 1, and the Palos Verdes, point 2, of Signal Hill are the terminals for the "upper Pleistocene" line.

Figure 2 frankly is a working hypothesis to be tested by new calculations based upon collections which have been carefully allocated in the local sections. Several preliminary tests have been made by analyzing published lists. For example, the median of the famous "Barlow Ranch" fauna near

Ventura is about 36°, according to Schenck & Keen (1937, p. 167). Consulting figure 2, one sees that this would fall either along the "upper Pliocene" or the "upper Pleistocene" line. An enquiry addressed to W. H. Holman elicited the statement (letter of July 6, 1943) that this fauna is younger than Timms Point bed 1, therefore younger than "upper Pliocene," and at the same time the beds with this fauna are not earliest Pleistocene. The Carpinteria terrace assemblage of Grant and Strong (1934) has a calculated median of 39°24′, thus coming between the "lower" and "upper" Pleistocene. The median (36°) of the small "upper Pliocene or lower Pleistocene" assemblage listed by Woodring in Hoots (1930, p. 120) from lower Rustic Canyon suggests an "upper Pliocene" age. Additional data will doubtless change the positions of the terminal points for the lines on the chart. Nevertheless, whatever the modifications, the general plan of translating faunal analyses into a calibrated median of midpoints scale should be of service in geology.

In summarizing the application of the index method of analysis to marine molluscan assemblages in western North America, the reader's attention again is drawn to the fact that the objective of this work is a finely-calibrated scale to measure environmental shifts along the Pacific Slope during late Cenozoic time. This objective has been approached by showing that the climatic-chronologic divisions in southern California can be expressed in terms of medians of mid-

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EXPLANATION OF PLATE 66

The photographs of specimens were supplied through the courtesy of the United States National Museum, Washington, D. C., except for the specimens deposited in the type collections of Stanford University and the California Academy of Sciences.

FIGS. *1–2*—*"Cyrtodaria" kurriana* Dunker, 1862. (Malak. Blätt., vol. 8, p. 38); Recent, Greenland.) Figured specimen, U. S. Nat. Mus. 366219; collected by R. S. Smith at Peard Bay, Alaska.

3–4—*"Lyonsiella" alaskana* Dall, 1895. (U. S. Nat. Mus. Proc., vol. 17, p. 703–705, pl. 25, fig. 2). Figured specimen (holotype), U. S. Nat. Mus. 123500; "Albatross" station 2859, in 1569 fathoms green ooze, southwest from Sitka in the Gulf of Alaska, bottom temperature, 34.9° F. Length 24 mm.

5–6—*Dacrydium pacificum* Dall, 1916. (U. S. Nat. Mus. Proc., vol. 52, p. 405.) Figured specimen, holotype, U. S. Nat. Mus. 214092, "Albatross" station 3604, Bering Sea, in 1401 fathoms. ×4.

7—*Myonera? tillamookensis* Dall, 1916. (U. S. Nat. Mus. Proc., vol. 52, p. 407). Figured specimen, holotype, U. S. Nat. Mus. 107819, "Albatross" station 3346, off Tillamook Bay, Oregon, in 786 fathoms. ×3.

8—*Lepton meröeum* Carpenter, 1864. (Brit. Assoc. Rept., p. 643.) Recent, San Diego-San Pedro area). Figured specimen (said to be the holotype by museum authorities, U. S. Nat. Mus. 15591, San Diego, California, collected by J. G. Cooper. ×5.

9–10—*Bornia retifera* Dall, 1899. (U. S. Nat. Mus. Proc., vol. 21, p. 889, pl. 87, fig. 2; Recent, off Santa Rosa Island, California, in 13 fathoms.) Figured specimen, U. S. Nat. Mus. 194141, San Miguel Island, California. ×4.

11–12—*Asthenothaerus villosior* Carpenter, 1864. (Annals and Mag. Nat. History, ser. 3, vol. 13, p. 311.) Figured specimen (said by museum authorities to be the holotype), U. S. Nat. Mus. 16292, Cape San Lucas, Baja California. ×3.

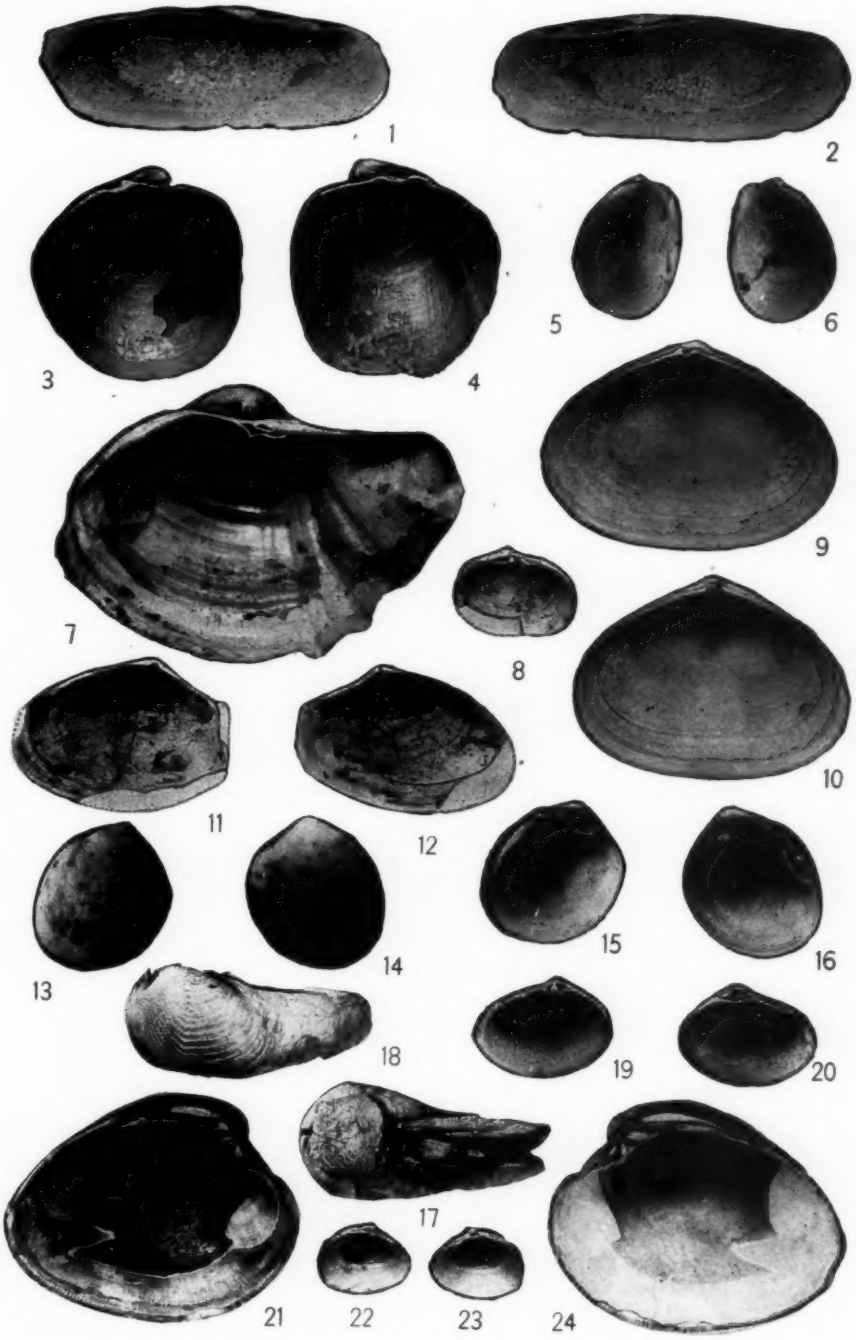
13–16—*Cyrilla munita* (Dall), 1898. (Wagner Free Inst. Sci. Trans., vol. 3, pt. 4, p. 602; Recent, Catalina Island, California, 30 fathoms.) Figured specimen, U. S. Nat. Mus. 211892, U. S. Bureau of Fisheries station 2901, off Santa Rosa Island, California, 48 fathoms. ×8.

17–18—*Martesia intercalata* Carpenter, 1855. (Mazatlan Cat., species no. 19, p. 13; Recent, Mazatlan, in *Spondylus lamarckii*.) Figured specimen, California Academy of Sciences type coll. no. 7231, Magdalena Bay, Baja California, Mexico. ×1¼.

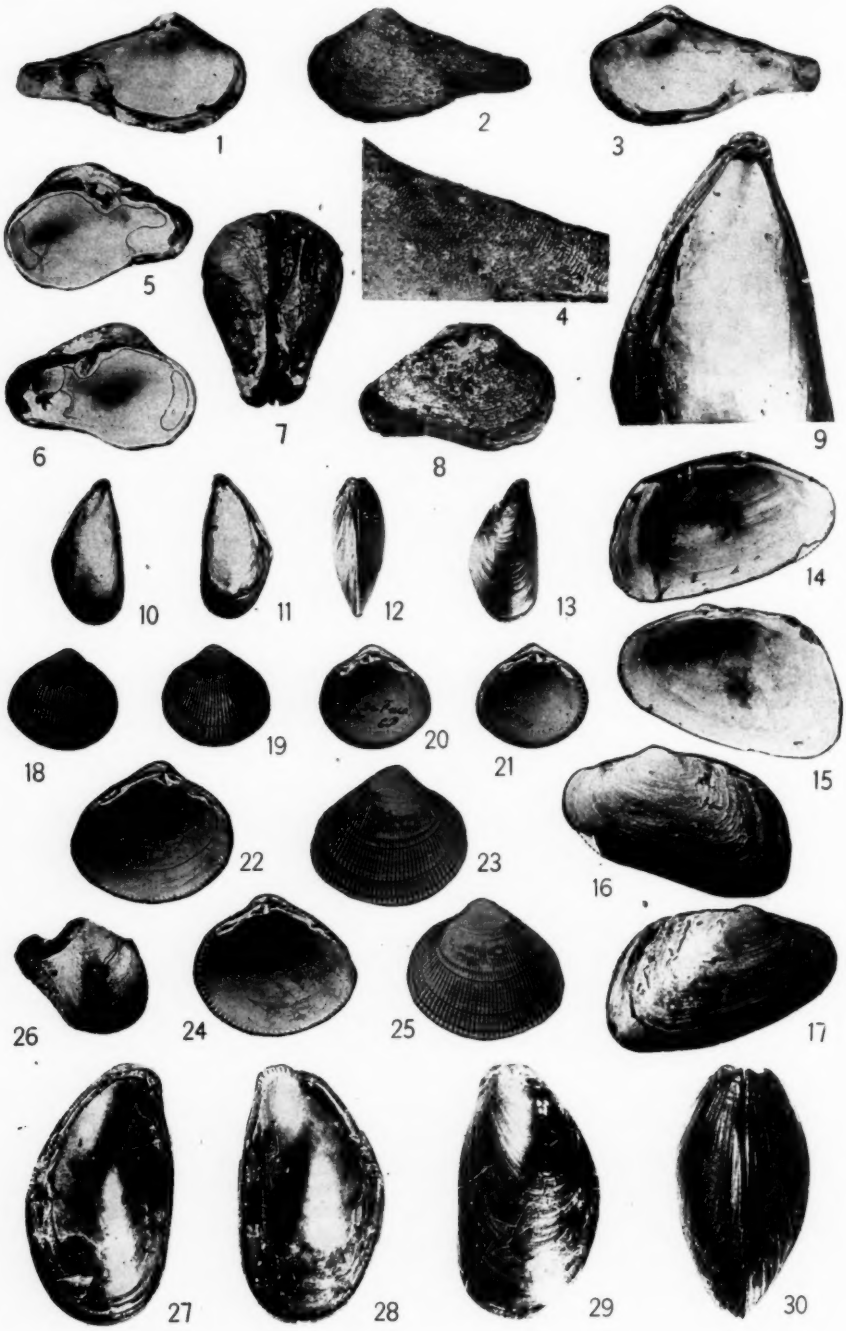
19–20—*Ervilia? californica* Dall, 1916. (U. S. Nat. Mus. Proc., vol. 52, p. 414.) Figured specimen, holotype, U. S. Nat. Mus. 151419, off San Pedro, California. ×2½.

21, 24—*Mercenaria kennicottii* Dall, 1871. (Am. Jour. Conchology, vol. 7, p. 147, pl. 16, fig. 1.) Figured specimen, holotype, U. S. Nat. Mus. 75017, Neah Bay, Washington, J. G. Swan, collector. Length 67 mm.

22–23—*"Anisodonta"? pellucida* Dall, 1916. (U. S. Nat. Mus. Proc., vol. 52, p. 411.) Figured specimen, holotype, U. S. Nat. Mus. 208475, off Del Monte, Monterey Bay, California, in 12 fathoms. ×5.



Schenck, Recent Pelecypoda



Schenck, Recent Pelecypoda

points of molluscan assemblages. Since the broad climatic (water temperature) divisions recognized for half a century can demonstrably be expressed in mathematical terms, it follows that finer divisions should be possible with added data.

Eastern North America

The index-method technique should be applicable to other coasts than the western coast of North America. A reconnaissance statistical investigation based on Johnson's (1934) list of the distribution of modern mollusks of the western North Atlantic Ocean suggests such a possibility. Midpoints were computed for the species on every tenth page of the list. The distribution of these is shown in figure 3. This curve, which shows the same fluctuations as the one for the eastern North Pacific Ocean, points to marine molluscan provinces centering near latitudes 30°, 40°, and 55° north. That is to say, one province centers along the coast of Northern Florida, one on the New Jersey coast, and one somewhere in Labrador. If subsequent analysis confirms this preliminary study, it would be necessary to revise the molluscan provinces as heretofore defined.

The implication of this analysis, further, is that the median-of-midpoint method could validly be used in interpreting the Pleistocene molluscan assemblages of the Atlantic seaboard. It would be interesting and perhaps instructive to verify the inferences made by Richards (1938), who employed somewhat subjective methods.

Collections made by the author at several localities in the western and southwestern Pacific Ocean after this paper was submitted for publication indicate that the method of analysis advocated here is applicable also to the western Pacific. The Indo-Pacific marine molluscan province, as originally defined, very probably encompasses much too great an area.

SURVEY OF FURTHER DATA REQUIRED

Any statistical technique such as this one is handicapped by lack of certain data. For the eastern Pacific area, at least, further research must be carried on before geologists are warranted in making more extended interpretations of molluscan distribution and of the conditions under which Cenozoic faunas may have thrived. Biostratigraphers who have attempted to draw paleogeographic inferences from biological evidence

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EXPLANATION OF PLATE 67

FIGS. *1–4—Plectodon scaber* Carpenter, 1864. (Brit. Assoc. Rept., p. 638, Recent, Santa Barbara Islands, California.) Figured specimen, topotype, Stanford Univ. Paleo. Type Coll. no. 6136, off Catalina Island, California, 40 fathoms, collected by G. Willett. Length 17 mm.

5–8—Sphenia globula Dall, 1919. (U. S. Nat. Mus. Proc., vol. 56, p. 570.) Figured specimen, paratype, Stanford Univ. Paleo. Type Coll. no. 6135, Bolinas Bay, California, collected by H. Hemphill. Length 15 mm.

9–13—Mytilus edulis trossulus Gould, 1850. (Boston Soc. Nat. History Proc., vol. 3, p. 344; Recent, "Killimook, Puget Sound, Oregon.") Figured specimen, topotype, Stanford Univ. Paleo. Type Coll. no. 6137, Cape Meares, Tillamook, Oregon, collected by A. M. Keen. Length 33 mm.

14–17—Saxicavella pacifica Dall, 1916. (U. S. Nat. Mus. Proc., vol. 52, p. 416.) Figured specimen, holotype, U. S. Nat. Mus. 209912, "Albatross" station 4356, off Point Loma, California, 120–131 fathoms. Length 5.3 mm.

18–21—Clinocardium blandum (Gould), 1850. (Boston Soc. Nat. History Proc., vol. 3, p. 276.) Figured specimen, holotype, U. S. Nat. Mus. 3899, Strait of Juan de Fuca, Washington. ×1.

22–25—Clinocardium fucanum (Dall), 1907. (Nautilus, vol. 20, p. 112.) Figured specimen, holotype, U. S. Nat. Mus. 42773, Strait of Juan de Fuca, Washington. This species is often confused with *C. californiense* (Deshayes), an Asiatic species which penetrates the North American coast only as far as the Alaskan Gulf area. Length 35 mm.

26—Navea subglobosa Gray, 1851. (Annals and Mag. Nat. History, ser. 2, vol. 8, p. 385; Recent, California.) Figured specimen, California Academy of Sciences Coll. no. 7232, Monterey Bay, California. Maximum diameter 6.4 mm.

27–30—"Modiolaria" phenax (Dall,) 1915. (Nautilus, vol. 28, p. 138.) Figured specimen, para type, Stanford Univ. Paleo. Type Coll. no. 6138, St. George Island, Pribiloff group, Bering Sea, collected by G. D. Hanna. Length 7 mm.

know how many pitfalls await them. They appreciate the cautionary remarks which Woodring (1938) and other writers have put before them. Some of the information which the writer thinks would add exactitude to the median analysis and inferences may be summarized in the following paragraphs.

(1) Specimens and water temperatures obtained from a large number of transverse profiles from the American coast into the deeper waters of the Pacific Ocean would add to the accuracy of the inferences. More data of a similar nature from the coastal bays are needed. Records of the frequency of specimens at individual collecting stations would be helpful.

(2) More shore collections should be obtained by collectors who distinguish between cast-up specimens and those found in the places where the animals lived. Equally does this apply to fossils. This implies that criteria should be set up for the recognition of autochthonous and allochthonous shells. For example, Woodring (1935, p. 299) pointed out that *Turritella jewetii* has been regarded by some authors as a living species despite the lack of records of living animals. Maybe some of the puzzling elements in the paleontologic record are due to reworked fossils.

(3) More sequences of fossil molluscan assemblages are needed in critical areas. The methods advocated by Schenck and White (1942) for collecting microscopic fossils could be applied more widely to the collection of mollusks. In this connection, W. H. Holman donated to Stanford University exactly the kind of collection desired, but unfortunately lack of time has prevented identification of the specimens.

(4) More spawning temperatures of eastern Pacific mollusks are needed. Facts of this kind will aid in the explanation of the causes underlying the formation of zoögeographic provinces.

(5) More data should be published on the ecology of modern Mollusca along the Pacific Slope. MacGinitie (1935, 1938, 1939) has contributed much valuable information and several conchologists are adding useful observations. When a detailed knowledge of local environments is thus added to the growing knowledge of submarine topography (Shepard and Emery, 1941), biostratigraphers will have a better basis for their conclusions.

The limitations imposed on the use of medians for interpreting individual faunal assemblages is in part due to local ecologic conditions. For example, a comparison of a Recent shore collection from Oregon with Alex Clark's list of species from the Timms Point formation shows a surprisingly small percentage of species in common. The majority of species in the Timms Point formation may live today in water several fathoms deep and are not often taken in shore collecting; the failure of the medians to select comparable communities merely emphasizes the necessity of dealing with assemblages from similar habitats.

(6) Bailey (1935) published an account of detailed geologic mapping which proved a lateral change in the fauna of the Santa Barbara formation in the vicinity of Ventura California. He stated, page 499:

> Therefore, the gradual progression of the warmer-water San Pedro type of fauna lower and lower into the stratigraphic column, from southwest to northeast (or south to north), indicates that the water became progressively shallower and the bottom sandier from southwest to northeast in the East Ventura area, and furnishes an excellent lower Pleistocene example of Natland and Clark's findings in the present San Pedro Channel.

Whether one draws the same inferences from the facts presented, workers agree that Bailey rightly urged caution in the application of paleontology to stratigraphic problems. As far as the present paper is concerned, the important fact which struck the writer when he studied Bailey's paper is that Bailey recognized "cold-water" and "warm-water" faunas. It is of comparatively little importance what formational name is applied to the strata in which those faunas are found, for the reason that geologists generally map rock-stratigraphic (cartographic) units and not "fossil" isothermal lines.

(7) Many taxonomic data are needed to facilitate the technique advocated in this paper. Several aspects of taxonomy that are relevant to the use of fossils in paleoecology may be mentioned briefly.

First, genera, species, and subspecies must be carefully discriminated if they are to serve the useful purposes of (a) defining dis-

tribution areas and (b) indicating depths at which were deposited geological formations. To make detailed discriminations, it helps to have illustrations of specimens, yet it may come as a surprise to some readers to learn that the accompanying two plates present for the first time illustrations of the interiors of several species named 28 and more years ago.

Second, if fine distinctions are made between species and subspecies, better use can generally be made of the mollusks as indicators of environment as well as of age. For example, consultation of plate 67, figures 9–13 will suggest that *Mytilus edulis trossulus* can be separated from *Mytilus edulis edulis*. When this separation is made, even so-called simple mussels are useful in zoögraphy, since by careful discrimination the subspecies *Mytilus edulis trossulus* is excluded from the Arctic fauna.

One of the striking examples of why species must bear correct names if check lists are to be meaningful can be taken from the pelecypod family Cardiidae. Specimens of *Clinocardium blandum* (Gould) (pl. 67, figs. 18–21) have been incorrectly called by several authors "*Cardium californiense* Deshayes," "*Laevicardium* (*Cerastoderma*) *californiense* Deshayes," and "*Cardium fucanum* Dall." Recognition of the two cardiid species figured on plate 67 clarifies a part of the "anomalous stratigraphy" of San Pedro in that the Arctic species "*Cardium*" *californiense* is eliminated from the Pleistocene record of southern California. The species of Cardiidae that do occur in the Timms Point formation live today in "cool temperate" waters along the coast from Sitka, Alaska, at least as far south as Monterey Bay, California.

Another example of the need for careful discrimination of species is furnished by *Martesia intercalata* (pl. 66, figs. 17–18). This has been confused in the past with the European species *Martesia striata*. If the American specimens are assigned to *M. striata*, then that species is cosmopolitan; if to *M. intercalata*, then the American specimens have some zoögeographic significance.

Plectodon scaber (pl. 67, figs. 1–4) has been incorrectly conceived by Oldroyd (1924, pl. 54, fig. 4), who figured a shell from Puget Sound under the name *Leiomya scabra* Carpenter. This shell actually belongs to a species of the genus *Cuspidaria*. If workers identify shells as *Leiomya scabra* by consulting Oldroyd, it is obvious that their shells would not bear the right name, that the range data would be incorrect, and that any resultant paleoecologic interpretations would be just that much wrong.

"*Modiolaria*" *phenax* (pl. 67, figs. 27–30), although named in 1915, is figured here for the first time. Dall (1915) pointed out in the original description of the species that these small shells might be mistaken for young specimens of *Mytilus* if not carefully examined.

Sphenia globula Dall (pl. 67, figs. 5–8) was named in 1919 for material from Bolinas Bay, California. It appears to be the same species as "*Cuspidaria*" *nana* Oldroyd, 1918 from Monterey. The correct name for the species is thus probably *Sphenia nana* (Oldroyd).

Finally, the nomenclature of many species and genera needs to be stabilized. Some names must be abandoned; many homonyms await renaming; other names should be protected (placed on the official list of *nomina conservanda*). Examine the footnotes to the tables accompanying this article and one will understand why stable nomenclature would be helpful. Keen (1937) used the generic name *Modiolus;* further research has convinced her that the correct name is *Volsella*, as Stewart (1930) had pointed out earlier. The troublesome matter of *Spirotropis* versus *Antiplanes* was mentioned in a footnote to table 2. The status of the names *Nassa* and *Nassarius* has been discussed by Woodring (1938, p. 26). These are only a few of the nomenclatural problems confronting taxonomists.

Although the biometrical analysis of molluscan assemblages is a valid technique applicable in stratigraphy, its application depends upon specimens, environmental data, and zoölogical names. Progress in the application of the technique will go hand in hand with progress in systematic collecting and taxonomy. As collectors bring in more specimens with more precise stratigraphic and ecologic information, as taxonomists reach agreement upon the delimitation and de-

nomination of species and genera, further analyses of molluscan distribution and its significance will be profitable.

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CORALS FROM THE OTTER FORMATION (MISSISSIPPIAN) OF MONTANA

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ABSTRACT—Two new species of *Caninia* are described, detailed descriptions of calices of *Triplophyllites spinulosus* are given, and *Pleurodictyum?* cf. *P. meekanum* is identified. Phylogenetic relationships of the new *Caninia* are discussed. The possibility is suggested that there may be a colonial trend in some groups of species of *Caninia*, which is phylogenetically separate from that of the simple forms.

INTRODUCTION

CORALS upon which this paper is based were collected by Mr. H. W. Scott from the upper part of the Otter formation. Two species of *Caninia* and one species of *Triplophyllites* were collected from black silty and sandy limestone with a pronounced hackly fracture. The locality is in the Ft. Logan quadrangle, on the north bank of the Missouri River, immediately west of the railroad junction of Lombard, and just downstream from the mouth of Sixteen Mile Creek; the corals occur in the upper part of a bed of limestone 47 feet thick, the top of which is 175 feet above the top of the Madison limestone. A schematic representation of the locality has been given by Scott (1935, column 8 of fig. 1, p. 1016).

The *Pleurodictyum* was collected from about 1 mile west of the quarry community of Eustis in the southern part of the Lombard Hills; the specimens occurred in a bed of brown limestone 1 foot thick, and about 19 feet lower stratigraphically than a bed of limestone 25 feet thick (which is equivalent to the 47-foot bed of the other locality). The beds at this place are overturned, hence, the top of the Madison is above the Otter. The *Pleurodictyum*-bearing bed is 207 feet higher stratigraphically than the top of the Madison.

The writer is indebted to Mr. H. W. Scott, of the Department of Geology and Geography, University of Illinois, for lending the material for description and for furnishing stratigraphic data.

CORRELATION

An assemblage of bryozoa, pelecypods, and numerous brachiopods identified by Scott from the Otter formation is indicative of Chester age. One of the species, *Sulcatopinna missouriensis*, is known most abundantly from the Menard limestone of the standard section in Illinois, although it is known from the Glen Dean limestone and the Clore formation as well. Subsequently, Scott (1942, p. 153) stated that the ostracodes (other than long-range species) from the Otter formation occur in Illinois in strata as low as Golconda and as high as Clore.

From the standpoint of corals alone, the age of the Otter seems to be Upper Chester. *T. spinulosus* is not of much value in stratigraphic studies because of its apparent long range. *P. meekanum* occurs in the Upper Chester of Arkansas and Oklahoma. The two species of *Caninia* are phylogenetically younger than a species from a Glen Dean correlative in the Appalachians, therefore, it is suggested on phylogenetic grounds that their age is Upper Chester.

SYSTEMATICS

Phylum COELENTERATA

Class ANTHOZOA
Order TETRACORALLA
Family CANINIIDAE
Genus CANINA Michelin in Gervais, 1840

Remarks.—For a complete discussion of this genus, see Easton (1944a, pp. 119–132). The two species described herein belong to the group of *Caninia cylindrica* referred to in that publication.

CANINIA BILATERALIS Easton, n. sp.
Figures 1, 2

Externals.—The corallite is trochoid and rather large with the cardinal fossula on the

convex side. The only specimen known to the writer was incomplete when obtained, hence it is not possible to say definitely what the habit was, although it appears to have been simple. The largest observed diameters were 47 by 39 (incomplete) mm. When complete, the specimen was probably more than 100 mm. long.

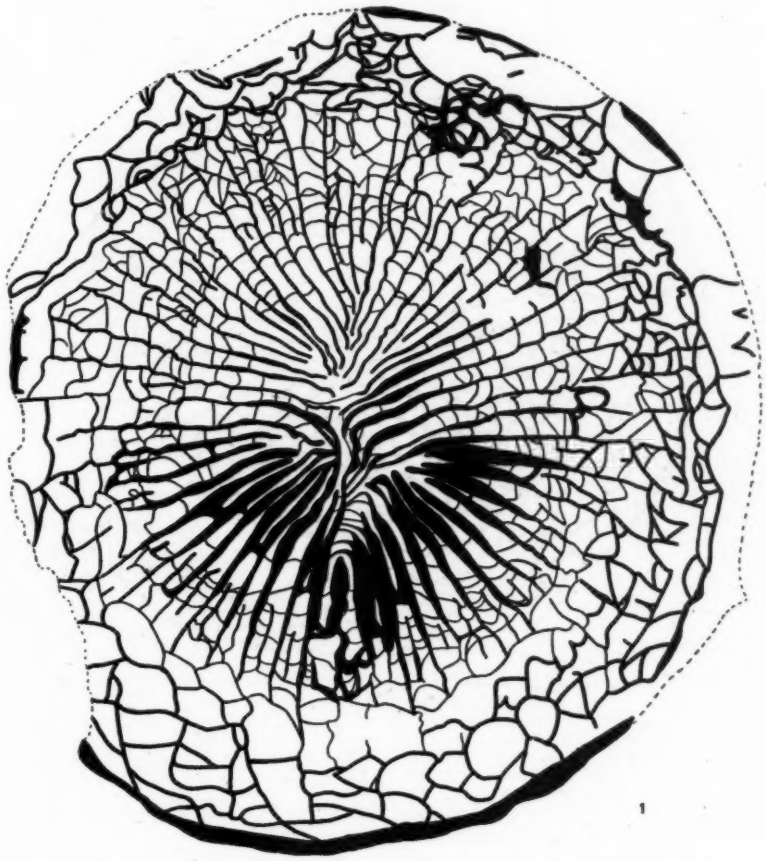


FIG. 1—*Caninia bilateralis* Easton, n. sp. Transverse section, late ephebic stage; holotype, ×2.75.

Transverse sections.—In late ephebic stage (diameters 41 by 37 mm.), there are 52 major septa, of which the 24 in the cardinal quadrants are more or less dilated within the tabularium. Thus, although the cardinal fossula is on the convex side, the concave side actually contains the greater number of septa. The cardinal and counter septa are each short, whereas the neighboring major septa are progressively longer, most of them reaching the axial region, thus providing strong bilateral symmetry. Minor septa extend a short distance into the tabularium. The dissepimentarium occupies half the radius and consists of an outer series of very large lonsdaleoid dissepiments and an inner series of heterogeneously formed dissepiments, the two series having a slight tendency to grade one into the other.

In middle ephebic stage, diameters 32 by 30 (incomplete) mm., there are 52 major septa arranged much as they are at the more advanced stage, except that a number of major septa in the left counter quadrant extend

across the center to become fused with or near the axial edges of some major septa in the right cardinal quadrant. Moreover, the line of demarcation between the inner and outer series of dissepiments is sharper than in the more advanced stage and the inner series tends largely towards the concentric pattern.

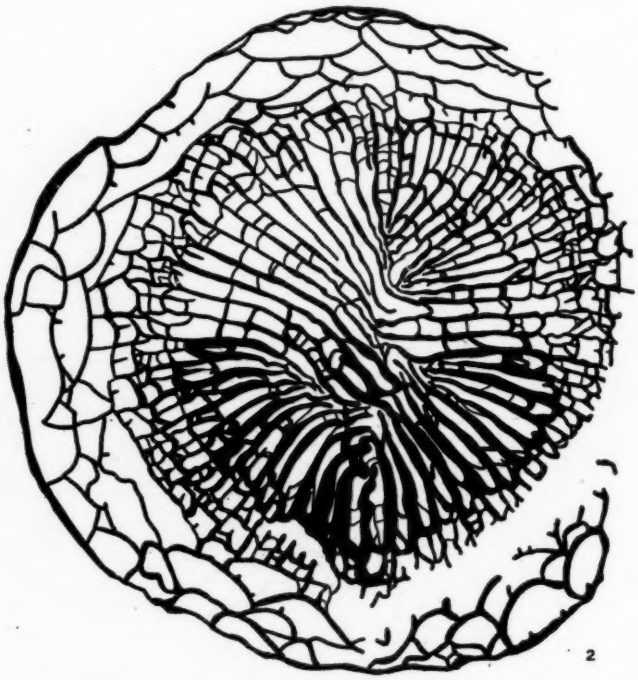


FIG. 2—*Caninia bilateralis* Easton, n. sp. Transverse section, middle ephebic stage; holotype, ×2.75.

At a somewhat earlier ephebic stage, diameters 25 by 24 (incomplete) mm., there are still 52 major septa, but most of them extend only about four-fifths of the radius and those in the cardinal quadrants are proportionately more dilated than they are in later stages.

Comparison.—*C. bilateralis* differs from mutation γ of the group of *C. cylindrica* illustrated by Vaughan (1915, pl. 3, fig. 4) chiefly in having longer major septa.

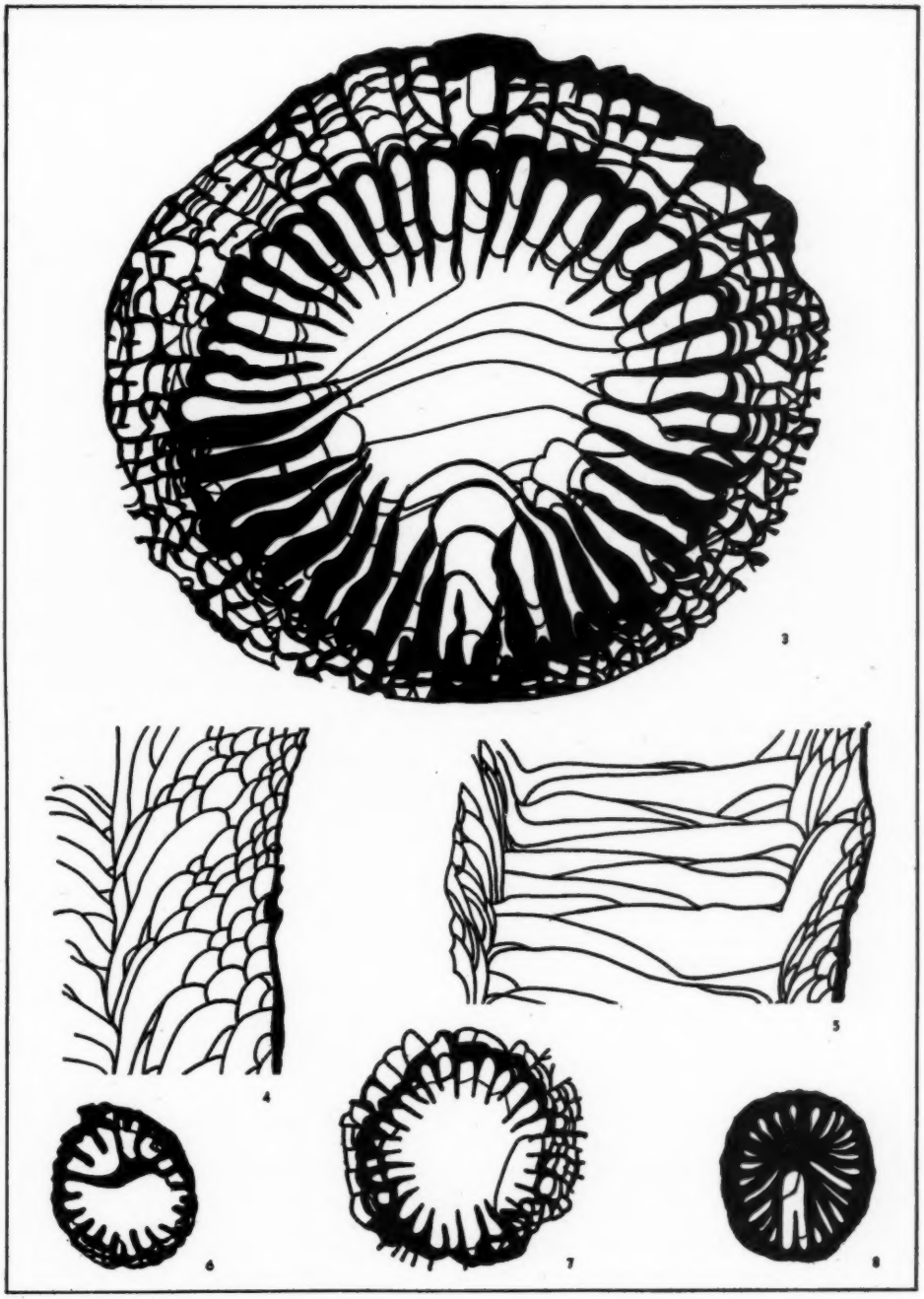
Material.—Holotype, University of Illinois no. X-1473.

CANINIA ENORMIS Easton, n. sp.
Figures 3–7

Externals.—The corallites are curved ceratoid to nearly cylindrical, occurring singly and also in parallel groups to form very loosely fasciculate colonies; when colonial, the corallites are joined near their tips in some instances and in other instances increase by mural budding. The cardinal fossula is on the convex side of the corallite The epitheca is thin, with prominent septal grooves, interseptal ridges, and well-developed rugae.

Apparently the calyx is exceedingly deep and vertically walled, but part of the notable depth may result from the breaking away of successive tabulae after death. Specimens vary in length from about 6 cm. to 10 cm. and in diameter from 3 to 4 cm., but one incomplete specimen is 6.5 cm. in diameter at the calyx and probably was more than 25 cm. in length.

Transverse sections.—In late ephebic stage, diameters 26.5 by 29 mm., the holotype has 40 major septa, of which the septa in the cardinal quadrants are dilated more than the remainder. Major septa extend three-fourths of the radius. Their portions



FIGS. *3–7*—*Caninia enormis* Easton, n. sp., ×3. *3*, Transverse section, late ephebic stage; holotype. *4*, Longitudinal section of dissepimentarium and outer edge of tabularium; paratype. *5*, Longitudinal section completely across the young portion of a corallite; paratype. *6*, Transverse section, very early ephebic stage; paratype. *7*, Transverse section, early ephebic stage; holotype. (p. 524)

8—*Triplophyllites spinulosus* (Milne-Edwards and Haime), ×3. Transverse section, early ephebic stage; plesiotype. (p. 526)

within the dissepimentarium are thinner than their portions within the tabularium. Moreover, the 18 major septa in the cardinal quadrants are on the convex side of the corallite. Minor septa extend a short distance into the tabularium in the cardinal quadrants, but elsewhere occur merely as septal ridges or as indistinct lines near the periphery of the dissepimentarium. The cardinal septum is short and is flanked by rather longer metasepta whose axial ends are joined by arches of tabulae across the cardinal fossula. Latest developed major septa of the counter quadrants are shorter than the previously developed major septa and are much thinner than the alar septa. The dissepimentarium extends one-third to one-fourth of the radius and consists of five to eight ranges of predominantly concentric and anguloconcentric dissepiments, although some pseudoherringbone dissepiments are present. A lonsdaleoid trend was not observed.

In early ephebic stage, diameter about 9 mm., the holotype has 28 somewhat dilated major septa and a few minor septa in the well-developed dissepimentarium.

In very early ephebic stage, diameters 5 by 6 mm., a paratype has about 23 major septa which extend half of the radius. Even at this early stage, traces of the dissepimentarium with included minor septa can be observed.

Longitudinal sections.—The tabulae are mostly incomplete and irregular in disposition, although they tend to be recurved proximally at their peripheries. Dissepiments are rather evenly concave near the epitheca but become elongate and arranged somewhat parallel with each other near the border of the tabularium. The tabulae have a density of 10 per cm.

Comparison.—*C. enormis* resembles *C. flaccida* Easton in habit of growth, but *C. enormis* differs from that species in having more dilated major septa and no lonsdaleoid dissepiments.

Material.—University of Illinois collection: holotype, no. X-1474; paratypes, nos. X-1475 to X-1478.

Family ZAPHRENTOIDIDEA Schindewolf, 1938

Genus TRIPLOPHYLLITES Easton, 1944

Remarks.—For a discussion of the characters of this genus and its relationships, see Easton (1944b, pp. 35–42).

TRIPLOPHYLLITES SPINULOSUS (Milne-Edwards and Haime)
Figure 8

Externals.—Curved ceratoid corals with interseptal ridges, septal grooves, and rugae. The cardinal fossula is on the concave side. Complete adult specimens measure about 5 cm. in length and 2.5 cm. in calycular diameter.

The calyx of well-preserved specimens is extremely deep and the epitheca is very thin in the distal portions.

The early ephebic stage in one specimen with a clean calyx has a proximally sagging cardinal septum in a very deep, axially expanded cardinal fossula. The right cardinal quadrant contains six major septa, the left cardinal quadrant contains five, the right counter quadrant contains eight, and the left counter quadrant contains seven major septa. The counter septum is somewhat longer than the other major septa. Minor septa are rudimentary. Major septa in the cardinal quadrants swing into parallelism with the trend of the cardinal fossula and tend to fuse along their inner portions. Alar septa are very prominent and are bordered on their counter sides by narrow alar pseudofossulae.

The same stage observed in another calyx has a slightly less axially expanded cardinal fossula. In the right cardinal quadrant the alar septum is prominent, bordered by a group of three and then a pair of major septa. The left cardinal quadrant has the prominent alar septum fused with two and bordered by a pair of major septa. Alar pseudofossulae are very prominent and axially expanded. The counter quadrants each have eight major septa on either side of the rather long counter septum. Minor septa are partially developed above the majors. This specimen shows three distinct periods of rejuvenescence.

A beekitized specimen at a somewhat later stage has 34 or 35 major septa, of which each cardinal quadrant contains eight septa. The cardinal septum is far down within the narrow cardinal fossula. Alar pseudofossulae are curved and narrow.

Still later on, a silicified calyx has a very short cardinal septum in a very narrow car-

dinal fossula. Each cardinal quadrant has eight major septa, but the somewhat thickened counter septum is bordered in the right counter quadrant by 11 major septa and by 10 in the left counter quadrant.

Transverse section.—The earliest stage observed has 25 major septa, an apparently short cardinal septum, and narrow alar pseudofossulae. The right cardinal quadrant has five, the left, four major septa, whereas, in the counter quadrants there are seven major septa on either side of a rather thick septum, which is probably the counter septum.

Material.—University of Illinois collection; plesiotypes, nos. X-1479 to X-1481.

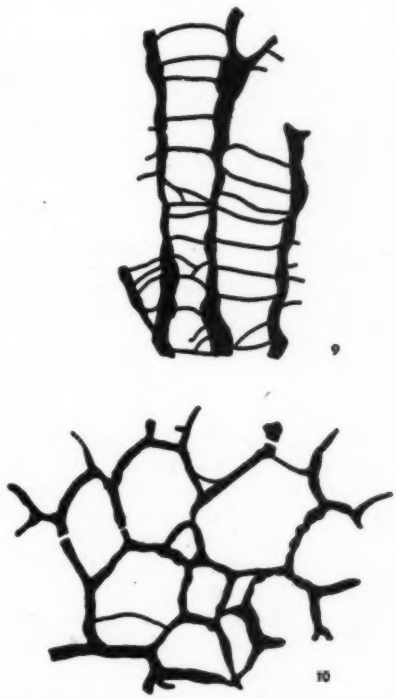
Remarks.—The specimens fall within the generally understood limits of variation of *T. spinulosus*, but these limits allow enormous latitude in identifications. It has not been feasible to collect adequate material for a thorough revision of this species; however, the writer has been able to arrive at tentative conclusions as to phylogenetic trends within the genus. Dissepiments, which are common in older species, become increasingly rare and may not even be present. The cardinal fossula changes from an axially expanded condition to a straight cleft. Alar pseudofossulae tend to become narrower, although always subject to great variation. Minor septa tend to be inserted earlier, although this is likewise quite variable.

Suborder TABULATA
Family FAVOSITIDAE
Genus PLEURODICTYUM Goldfuss, 1829
PLEURODICTYUM? cf. P. MEEKANUM (Girty)
Figures 9, 10

Michelinia meekana GIRTY, 1910, New York Acad. Sci. Annals, vol. 20, no. 3, p. 189.
Michelinia meekana, SNIDER, 1915, Oklahoma Geol. Survey Bull. 24, pt. 2, p. 71, pl. 3, figs. 9–11.
Michelinia meekana, Easton, 1942, Arkansas Geol. Survey Bull. 8, p. 84.
Pleurodictyum meekanum, Easton, 1943, Jour. Paleontology, vol. 17, no. 2, pp. 130, 136.

Remarks.—Several fragments of a colonial tabulate coral are tentatively identified as *P. meekanum*. In transverse section the corallites are irregularly shaped, about 4 mm. in diameter. In longitudinal section there are about nine tabulae in 1 cm. Mural pores were seen only rarely and it is not known whether their scarcity is due to poor preservation or is actually caused by a major morphologic difference between this specimen and true *Pleurodictyum*.

Material.—University of Illinois no. X-1482.



FIGS. *9*, *10*—*Pleurodictyum?* cf. *P. meekanum* (Girty), ×3. *9*, Transverse section. *10*, Longitudinal section.

PHYLOGENETIC CONSIDERATIONS

Caninia enormis Easton is very similar to mutation[1] δ of the group of *C. cylindrica* as figured by Vaughan (1915, pl. 3, fig. 5), and *C. bilateralis* Easton is rather similar to mutation γ of the same group as figured by Vaughan (idem, fig. 4). It is worthwhile to discuss the relationships of these specimens because it would appear either that the colonial corals concerned constitute a phylogenetic series among themselves or that the colonial habit was derived in each case from the stock of simple habit.

Both of Vaughan's mutations just mentioned occur in the lower Visean faunal zones

[1] Mutation is used here in the prior (paleontological) sense as defined by Waagen and not in the sense as applied by practically all geneticists. See Mayr, 1942, p. 65.

S_1 and upper C_2 and are thought to represent the species group as it appeared after the group migrated from Belgium into England. Vaughan's phylogeny was based upon certain variations as follows (Vaughan, idem, p. 37).

> . . . the variable which registers the progression most clearly is the width of the ring of small septi-vesicles just outside the inner wall. [The same fact may be expressed in several ways, as, for example:—
>
> (1) The extent of the backward prolongation of the septa from the inner wall.
>
> (2) The width of the ring of intermediate septa.
>
> (3) The diminution in the peripheral zone of large vesicles.]
>
> The law of development of the variable may be thus expressed:—
>
> The width of the ring of septi-vesicles increases from practically zero at β^2 up to the whole area between the walls at δ. There is also a gradual increase in the size of the corallum.

Caninia enormis, with its tendency toward colonial habit apparently represents a much later development of the species group than one would imagine from comparison with the figure of mutation δ mentioned above. It is generally thought that S_1 and upper C_2 are equivalent to part of the Iowa series of the standard Chester section in Illinois, whereas it has already been pointed out that the Otter formation is equivalent in part to about upper middle and upper Chester. A similar instance was cited by Lewis (1935, p. 122), who considered *Caninia veryi* possibly to be "a later phaceloid development of the *C. juddi* stock." The writer wishes to point out here again that there is no proof that *C. veryi* is not a member of a stock of corals with colonial habit which paralleled the development of the simple-habit *C. juddi* stock. In any case, the evidence in these two cases points to emergence of morphologic features characteristic of simple corals in stratigraphically younger colonies of corals. Phylogenetic trends toward development of increasingly compact colonies of corals have long been known in the literature, but the writer is not aware of any published comparisons of phylogenetic similarity between simple and compound corallites. Indeed, it probably is not possible at this stage to carry the investigation much further. The only feature of neontology which may bear upon the subject, in so far as the writer is informed, is Mayr's reference (1942, p. 73) to the work of Vavilov and others, who contend that phylogeny is indicated to a certain extent among related species having mutations (geneticists' mutations) of like nature. Vavilov's suggestion has been especially applicable in polymorphic groups.

It is most interesting to note, however, that *C. flaccida* Easton, from an equivalent of the Glen Dean limestone in the Appalachians, could occupy approximately the same phylogenetic position with regard to *C. enormis* as mutation κ does to mutation δ in the *C. cylindrica* species group illustrated by Vaughan (idem, pl. 3, figs. 1, 5).

[2] The earliest mutation figured by Vaughan and having very large lonsdaleoid dissepiments and thin septa.

MANUSCRIPT RECEIVED MARCH 18, 1944.

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JOURNAL OF PALEONTOLOGY, VOL. 19, NO. 5, PP. 529–533, PLS. 68, 69, SEPTEMBER 1945

SOME SILURIAN TRILOBITES FROM PORT DANIEL, QUEBEC

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ABSTRACT—*Cheirurus tarquinius*, *Scutellum pompilius*, *Dicranopeltis canadensis* and *Ceratocephala goniata* are reillustrated. The latter two are shown to be ornamented with scattered spines, the bases of which have formerly caused their ornamentation to be referred to as tuberculate.

THE TRILOBITES described here have resulted from Dr. Stuart A. Northrop's discoveries of fossil localities in the Port Daniel Region of the Gaspé Peninsula, from Dr. G. Arthur Cooper's calling the writer's attention to several of these localities, and from the writer's predilection for collecting good specimens of trilobites.

In using Northrop's paper for identification the writer has found that several of his specimens present unusual features hitherto unrecognized. New illustrations are presented to show these features.

To summarize this new information: a cephalon of *Scutellum pompilius* (Billings) shows several features that have been misrepresented in previous illustrations and in addition shows the genal angle; *Dicranopeltoides? logani* Northrop is regarded as a synonym of *D. canadensis* (Logan), the posterior of the pygidium is illustrated, and the tubercles on its surface are shown to be the bases of short spines which covered the pygidium; *Ceratocephala goniata* Warder is shown to have similar short spines and to be more closely allied in other ways to the Bohemian species *C. verneuilli* (Barrande) than was formerly supposed; and *Cheirurus tarquinius* Billings is reillustrated to give a better conception of this, "the world's largest cheirurid."

The *Cheirurus* came from Northrop's locality 55, 1½ miles southwest of West Point, Port Daniel. The other species came from Northrop's locality 19, the brachiopod limestone in the fields above Reddish Point on the west side of Anse au Gascons. The specimens, collected, cleaned, and photographed by the writer, belong in his private collection.

Genus SCUTELLUM Pusch, 1833
(=*Goldius* de Koninck, 1841; *Bronteus* Goldfuss, 1843; *Thysanopeltis* Hawle and Corda, 1847)

SCUTELLUM POMPILIUS Billings
Plate 69, figures 1–3

Brontes sp. LOGAN, 1844, Canada Geol. Survey Rept. Prog., p. 54.
Bronteus canadensis (part) LOGAN, 1863, Canada Geol. Survey Rept. Prog., p. 444.
Bronteus pompilius (part) BILLINGS, 1869, Portland Soc. Nat. History, Proc., vol. 1, pt. 2, p. 123, pl. 3, fig. 25.
Goldius pompilius (Billings) NORTHROP, 1939, Geol. Soc. America Special Papers no. 21, p. 231, pl. 25, figs. 1–4.

Northrop gives an account of the synonomy of this species. He points out that Billings' species was based partly on specimens from Port Daniel and partly on Devonian specimens from Square Lake, Maine. Northrop restricts the species to the Silurian form and reproduces Billings' original figure and description.

Cephalon: The head illustrated here differs from Billings' figure and description. The eye is larger and extends closer to the posterior border. The eye has many facets, which are plainly visible under the microscope. A curving furrow runs forward from a point directly behind the eye inwards to the axial furrow opposite the third pair of glabellar furrows. The occipital ring has a small median tubercle. Its posterior margin is not straight, as Billings shows it, but extends more posteriorly at the axis than at the sides. The genal angle, unknown to Billings is preserved on this specimen. The free cheek is convex for about half the distance from

the eye to the border and is concave on the outer half of that distance.

Thorax: Although Billings stated that the thorax was unknown, his illustration shows it restored. The three thoracic segments illustrated here show that the rachis and inner portions of the pleurae are almost straight. The outer portions of the pleurae, however, turn posteriorly more than Billings restoration indicates.

Pygidium: Northrop figured a pygidium that shows several differences from Billings' pygidium from Square Lake. The pleural furrows are concave anteriorly instead of posteriorly. There is a short, faint median furrow posterior to the rachis. The elevated portion of the rachis has parallel sides, which, however, do not extend to the anterior border. The pygidium illustrated here has a complete border. Its outline is more elliptical than Billings showed it. Figure 3 is a photograph of its concave impression in the limestone.

Genus DICRANOPELTIS Hawle and Corda, 1847

Phleger erected a number of new genera in his paper on lichadian trilobites. One of these is *Dicranopeltoides*, and to this genus Northrop doubtfully referred logan's *Lichas canadensis*. This species does not fall, however, into either *Dicranopeltis* or *Dicranopeltoides* as Phleger defines these genera, but combines features of both. In *Dicranopeltoides* Phleger says the axial lobe of the pygidium narrows posteriorly to a point. The Port Daniel species has a rounded posterior.

Dr. Elsa Warburg (1939) notes that the classification of the Lichadidae is exceedingly difficult and expresses dissatisfaction with Phleger's results. She places Phleger *Dicranopeltoides* and *Maromuktis* in the genus *Dicranopeltis*, for which she gives the following diagnosis:

> Cranidium with complete dorsal furrows; prolonged anterior lateral glabellar furrows not reaching occipital furrow, basal portion of median lobe defined at sides only by weak grooves or slight depressions; basal lateral glabellar furrows well defined; occipital lobes well defined. Pygidium with prolonged dorsal furrows dying out before reaching margin, or growing weak posteriorly and ending and nearly meeting at fork between free terminations of basal pair of pleurae; rachis with two ring furrows, rather indistinctly defined behind, continued by long post-rachial piece; pleural portions composed of three pairs of furrowed pleurae ending in free points.

The specimens from the Port Daniel region may differ from this definition in that the presence or absence of occipital lobes is not certain.

DICRANOPELTIS CANADENSIS (Logan)
Plate 69, figures 6–9

Brontes? canadensis LOGAN, 1846, Canada Geol. Surv. Rept. Prog. 1844, p. 53, figure of cephalon.

Lichas canadensis (Logan) LOGAN, 1863, Canada Geol. Surv. Rept. Prog. to 1863, p. 444.

Dicranopeltoides? canadensis (Logan) NORTHROP, 1939, Geol. Soc. America Special Papers no. 21, p. 235, pl. 26, figs. 1–5.

Dicranopeltoides? logani NORTHROP, idem., p. 237, pl. 26, figs. 6, 7.

Northrop gives an account of the synonymy of this species and reproduces Logan's drawings of the cephalon and the pygidium. Logan's drawings were "not taken from one specimen, but made up from several, namely, two of the head and four of the tail."

Since only one kind of head and only one kind of pygidium have been found associated here, it is best to consider them the same species.

Logan's drawing of the pygidium should be rejected from serious consideration. It does not have the three pairs of free pleural points or spines characteristic of *Dicranopeltis* which Northrop mentions in his specimens and which occur in the writer's. Northrop did not figure the posterior part of the pygidium of any of his specimens. Assuming that the anterior half he illustrated is the same species as the pygidium figured here, the outline of the entire pygidium can be reconstructed in a rough manner as in figure 8. The dorsal furrows converging posteriorly do not meet but remain separated, where they end near the bases of the third pair of pleural free points. Small spines rise from the surface tubercles where the limestone has not been cleaned away. This specimen shows the pygidium to have been covered by small spines. It is probable that the head was similarly ornamented. These

spines may exist in other species but may not have been noticed where preservation is less perfect.

The fragmentary heads in my collection are more complete than those Northrop illustrated and as far as they are preserved agree with Logan's drawing. This species most closely resembles *D. decipiens* Winchell and Marcy but may differ, as no occipital lobes are preserved. If future specimens should prove Logan's drawing incorrect as was his drawing of the pygidium, this species would better conform to the definition of *Dicranopeltis*.

Genus CERATOCEPHALA Warder, 1833

The genus *Ceratocephala* was erected by Warder (1838) for his new species *C. goniata*. He had his specimen reversed and considered the two occipital spines (the only one preserved on his specimen) to correspond with the antennae of modern crustaceans.

Weller (1907) redefined the genus as follows:

> In the characters of the glabella and cheeks the members of this genus closely resemble *Acidaspis* and *Odontopleura*, but the occipital segment bears two divergent spines which are separate at their bases.

Raymond discarded the classification on the basis of spines in his paper on "The genera of the Odontopleuridae." His definition of *Ceratocephala* is given as

> . . . free and fixed cheeks anchylosed, eyes far forward and far from the glabella. The pleural lobe of each thoracic segment is divided by a shallow median furrow into equally elevated portions. Silurian. Europe and North America.

In this genus he places only two American species, *C. depauperata* Van Ingen and *C. goniata* Warder.

The Port Daniel *Ceratocephala* was first at thought to be a new species, for it seemed to differ markedly from Weller's beautiful illustration, which has been reproduced by Northrop and, more recently, in "Index Fossils of North America." A comparison of the Port Daniel specimen with Hall's type of *Acidaspis danai* and a squeeze of Winchell and Marcy's *Acidaspis ida* in the American Museum of Natural History leaves no doubt that these are the same species.

CERATOCEPHALA GONIATA Warder
Plate 69, figures 4, 5

Ceratocephala goniata WARDER, 1838, Am. Jour. Sci., vol. 34, p. 377.
Acidaspis danai HALL, 1862, Wisconsin Geol. Survey, vol. 1, p. 432 (no description); 1865, New York State Cab. Nat. History 18th Rept., p. 28, adv. sheets; 1868, idem 20th Rept., p. 333, pl. 21, figs. 8, 9; 1870, idem, revised edition, p. 423, pl. 21, figs. 8, 9.
Acidaspis ida WINCHELL and MARCY, 1865, Boston Soc. Nat. History Mem., vol. 1, p. 106, pl. 3, fig. 13.
Ceratocephala goniata, Clarke, 1892, New York State Mus. Nat. History, 44th Rept., pp. 91–100, pl. 1, fig. 1.
Ceratocephala goniata, KINDLE, 1904, Indiana Dept. Geology and Nat. Resources, 28th Ann. Rept., p. 480, pl. 24, fig. 13.
Ceratocephala goniata, Weller, 1907, Chicago Acad. Sci. Bull., no. 4, pt. 2, p. 255, pl. 23, fig. 1, 2.
Ceratocephala goniata, RAYMOND, 1913, Victoria Memorial Mus. Bull., vol. 1, p. 38.
Ceratocephala goniata, RAYMOND, 1916, Harvard College Mus. Comp. Zoology Bull., vol. 60, no. 1, p. 24.
Ceratocephala goniata, NORTHROP, 1939, Geol. Soc. America Special Papers no. 21, p. 238, pl. 28, figs. 1, 2.

The obvious differences between the Port Daniel specimen, figures 4 and 5, and Weller's illustration are: three pairs of glabellar furrows (Weller showed two); a narrow brim in front of the glabella (Weller showed none); the posterior band of the occipital ring is not visible from the front view (Weller shows it); on well-preserved specimens small spines form a fringe around the border. In cleaning the specimen it was observed that similar spines pointed up at right angles to the outer fringe. All that remains of these upright spines after removing the limestone from the border are the tubercles which represent their bases. The presence of tubercles suggests that these small spines were scattered over the entire cephalon. This spiny ornamentation is similar to that described above in *Dicranopeltis canadensis*. Perhaps many other trilobites that are described as having a tuberculated surface likewise had a spiny ornamentation. Good preservation and care in cleaning specimens under a binocular microscope may determine such a condition.

C. goniata closely resembles *C. verneuilli* (Barrande). It differs in several particulars.

First, the glabella merges with the fixed cheeks so that the boundary between them cannot be definitely determined. Second, the marginal spines are in more than one row along the border; some, broken off in uncovering the specimen, point up almost at right angles to those directed outwards, which are still preserved. Third, a median bump is situated on the glabella a little anterior to the third pair of glabellar lobes. This bump is covered by tubercles like the rest of the head. There are other distinctions of which one cannot be certain without specimens for comparison. For instance it appears that *C. goniata* has deeper furrows marking off the occipital lobes.

C. goniata has the same structure of the occipital ring that Warburg (1933) pointed out to be present in *C. vesiculosa* (Barrande). This structure supports her concept that the occipital ring is more than the narrow posterior band that Reed considered it.

Genus CHEIRURUS Beyrich, 1845
CHEIRURUS TARQUINIUS Billings
Plate 68, figures 1–5

Cheirurus tarquinius BILLINGS, 1869, Portland Soc. Nat. History Proc., vol. 1, part 2, p. 121, pl. 3, fig. 22.
Cheirurus tarquinius, WILLIAMS, 1900, U. S. Geol. Survey Bull. 165, pp. 33, 52.
Ceraurus tarquinius, WHITEAVES, 1906, Canada Geol. Survey Paleozoic Fossils, vol. 3, part 4, p. 267.
Cheirurus tarquinius, RAYMOND, 1916, Harvard Coll. Mus. Comp. Zoology Bull., vol. 60, no. 1, p. 38.
Cheirurus tarquinius, Northrop, 1939, Geol. Soc. America Special Papers no. 21, p. 241, pl. 27, figs. 1–7; pl. 28, figs. 3–6.

This beautiful trilobite was known to Billings only from a small incomplete cranidium. Northrop has improved our knowledge of it by finding a medium-sized complete individual with eleven thoracic segments. In addition he illustrates fragments of larger individuals. These illustrations do not, however, do justice to this, "the world"s largest cheirurid," nor do they convey an adequate conception of its shape.

The two cranidia on plate 68 are the first illustrations to show the cranidium with its attached genal spine. Figure 1 shows the very highly elevated occipital ring. This hitherto unnoted feature accounts for this portion being broken from most of the specimens collected. Similarly the very elevated rachis results in that part of the thoracic segments and of the first segment of the pygidium being missing from most specimens. The articulating ring of the first thoracic segment shows beneath the broken occipital ring in figure 3. *C. tarquinius* was a very strongly constructed trilobite. The segments articulate not only at the rachis, but articulating teeth and sockets are provided halfway out on each pleuron. This articulating arrangement extends to the anterior border of the pygidium and the posterior border of the fixed cheek. Halfway out the posterior border of the fixed cheek is highly raised; behind this is a depression followed by a small knob. This knob corresponds to a similar knob on the posterior margin of a thoracic pleuron and fits over a projection on the anterior margin of the succeeding segment. Thus each segment has three hinges on the anterior and three on the posterior border to keep it firmly in place. The spines of the pygidium are nearly flat on the dorsal surface but are very convex on the ventral surface so that they have considerable thickness and strength.

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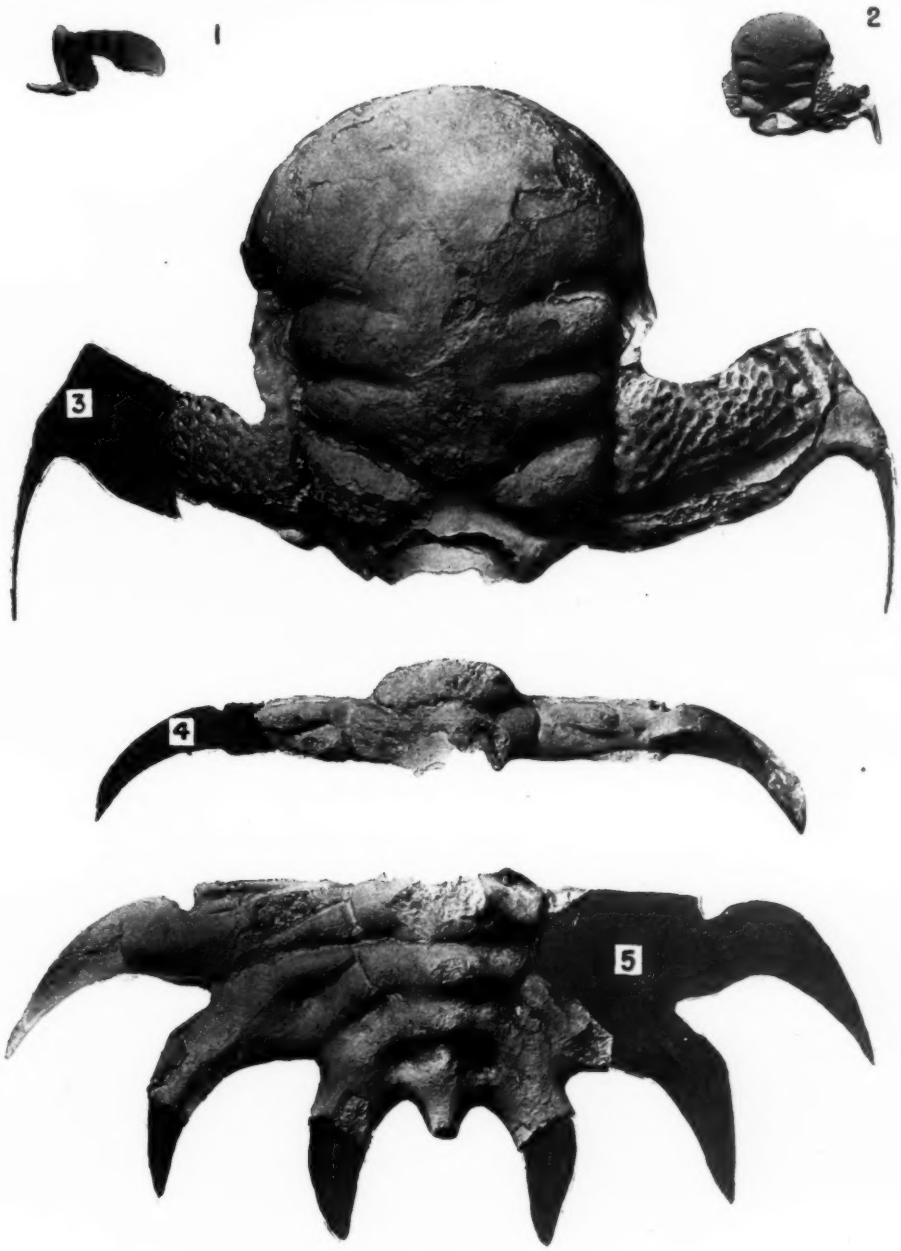
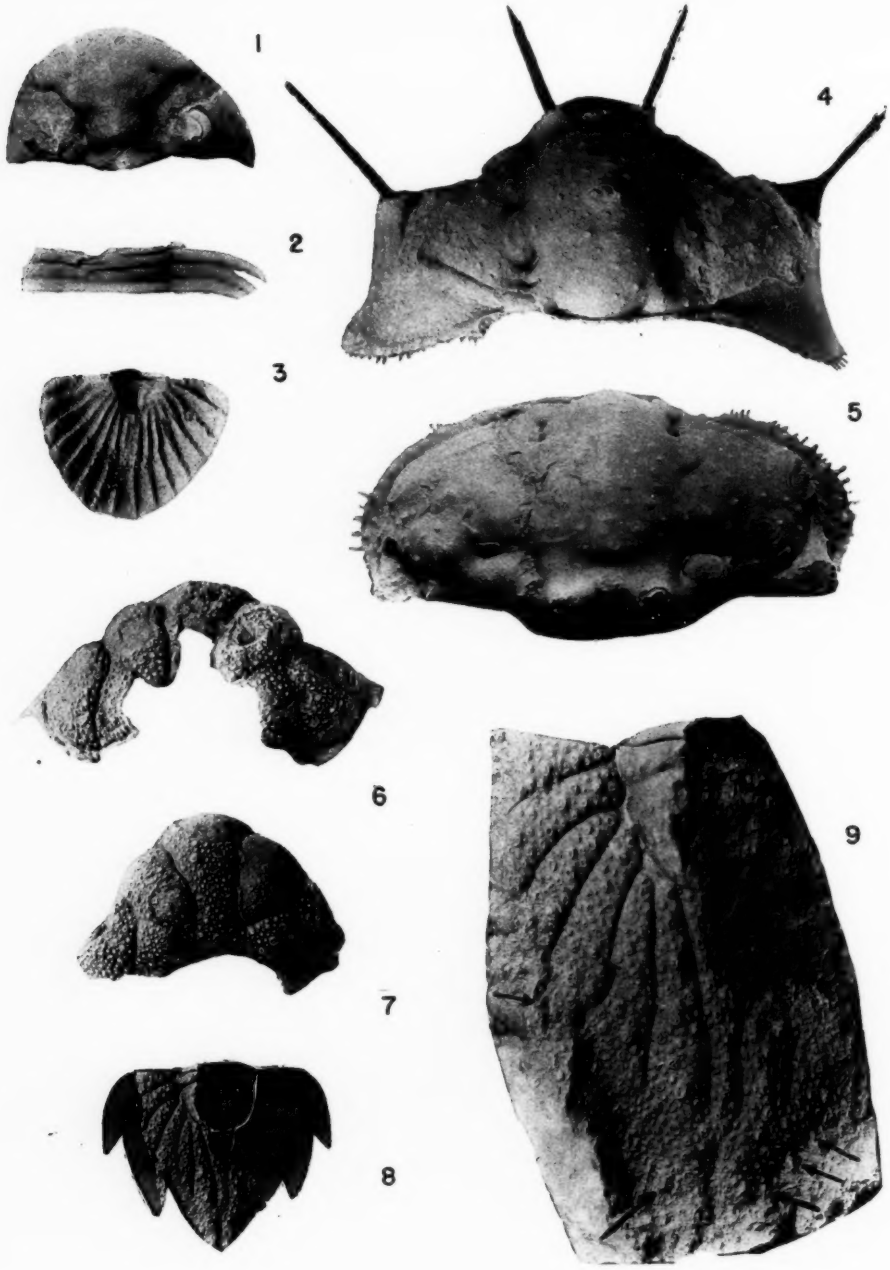
RAYMOND, P. E., 1916, New and old Silurian

EXPLANATION OF PLATE 68

FIGS. *1–5*—*Cheirurus tarquinius* Billings, ×1. *1, 2*, Side and dorsal views of a small cranidium. *3*, Large nearly complete cranidium. *4*, Thoracic segment of a somewhat smaller individual. *5*, Large pygidium, shape of spines reproduced from impressions in the rock split off above this specimen. (p. 532)



Kindle, Silurian Trilobite



Kindle, Silurian Trilobites

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MANUSCRIPT RECEIVED JUNE 30, 1944.

EXPLANATION OF PLATE 69

FIGS. *1–3—Scutellum pompilius* Billings, ×2½. (p. 529)
4, 5—Ceratocephala goniata Warder, ×2½. *4*, Front view with position of large spines roughly indicated. *5*, Dorsal view of the same specimen. (p. 531)
6–9—Dicranopeltis canadensis (Logan). *6, 7*, Incomplete heads, ×2½. *8*, Incomplete pygidium, ×2½. *9*, Same specimen as preceding, arrows point to some of the small spines rising from surface of the pygidium, ×7. (p. 530)

JOURNAL OF PALEONTOLOGY, VOL. 19, NO. 5, PP. 534–538, PL. 70, SEPTEMBER 1945

PACHYCEPHALOSAURIDAE PROPOSED FOR DOME-HEADED DINOSAURS, STEGOCERAS LAMBEI, N. SP., DESCRIBED

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L. M. LAMBE (1902) described the frontoparietal mass of a dome-headed dinosaur as *Stegoceras validus*. At that time he considered his specimen to be a median part of the skull in front of the nasals, and tentatively referred it to the Ceratopsia. In 1918 the same author described a well-preserved dome and surrounding bones of a young individual. In this paper he showed for the first time that the dome or frontoparietal mass was composed of thickened cranial bones and not of dermal scutes fused with the cranial bones. Most of the sutures were discernible, and Lambe gave very complete information about the cranial bones. This specimen showed the presence of a postfrontal bone as distinct from the postorbital, an unusual occurrence in Upper Cretaceous dinosaurs.

In 1924 Gilmore described the first complete skull of a dome-headed dinosaur from the same beds, i.e. the Oldman (Belly River) formation of Alberta, Canada. This specimen (no. 2, University of Alberta collections), which also has accompanying skeletal parts, was identified as *Stegoceras validus* Lambe. Gilmore (1924, pp. 9–10) stated, however, that the premaxillary teeth were generically indistinguishable from Leidy's type of *Troödon* (*T. formosus*) and that, consequently, *Stegoceras* was a synonym of *Troödon*.

Brown and Schlaikjer (1943) described a second complete skull of a dome-headed dinosaur, which they placed in a new genus "*Pachycephalosaurus*." This generic name happily stresses the thick-skulled character of the animal. Their treatment of the "troödonts" is very complete, all the important specimens assigned to the group being well illustrated and discussed. There are, however, some taxonomic interpretations with which, for reasons here presented, the writer is not in full accord.

Brown and Schlaikjer (1943, p. 128) followed Gilmore in regarding *Troödon* and *Stegoceras* as synonymous, but state that they "believe that *T. formosus* and *T. validus* are at least specifically distinct." They pointed out (1943, p. 127) that

> the *T. formosus* tooth has the central area of the outer surface anteroposteriorly convex, while in *T. validus* the outer surfaces of the premaxillary teeth are vertically ribbed. It also lacks the conspicuous posterior "heel" that is characteristic of the teeth of *T. validus*, and the marginal denticulations are much better developed.

In the collections of the Geological Survey of Canada there are eight loose teeth from the Oldman (Belly River) and Edmonton formations on Red Deer River, Alberta, which are very similar to the type of *Troödon formosus* Leidy. Lambe (1902, p. 47) identified two of these as *Troödon formosus*, and briefly described one (G.S.C. no. 1267).

Through the courtesy of Dr. H. G. Richards, associate curator of Geology and Paleontology, Academy of Natural Sciences, Philadelphia, the writer received a cast of the type of *Troödon formosus* Leidy. A study of this and of Leidy's (1860, pl. 9, figs. 53–55) illustrations enabled him to confirm Lambe's identification of the loose teeth, G.S.C. nos. 1266 and 1267, as *Troödon*. The G.S.C. teeth differ from Leidy's type (pl. 70, fig. 1) in minor details, which at most could be regarded only as specific differences. Tentatively, at least, all are referred to *Troödon formosus*. These teeth are slightly less pointed than shown by Leidy, but an examination of the cast suggests that Leidy's figures show his specimen too pointed. In G.S.C. no. 1267 (pl. 70, fig. 2) and also in specimen no. 8841 (pl. 70, fig. 3) the crown, except the tip, is complete, and when compared with the type it shows that practically nothing is missing from the base of the crown of Leidy's specimen.

In the type of *T. formosus*, as well as in the loose teeth referred to above, the crown is completely enamelled, compressed, curved

conical, and the edges are studded with coarse denticles. The denticles themselves are compressed cones, but there is no sign of these extending onto either face of the crown as even the faintest of flutings. These faces are convex anteroposteriorly and are perfectly smooth, and there is no enlargement of the base of the crown. It is evident that the root, or fang, of the tooth was not constricted, but was simply a thin-walled, unenamelled extension of the crown. Wear shows near the center of the inner? face, extending from the apex as a long, narrow plane, in G.S.C. no. 8841 more than halfway to the base of the crown.

All the above-mentioned characters are typical of maxillary and dentary teeth of the carnivorous dinosaurs, except that the denticles are coarser and more ornamented than usual. Similarity of wear and cross section of the crowns in *Troödon* and the carnivorous dinosaurs may be seen by reference to Leidy's (1860, pl. 9, figs. 29–32 and 54–55) figures. Indeed Nopcsa (1901, p. 255) referred *Troödon* to the Megalosauridae, and Hay (1902, p. 147) also placed it under that family. It would now appear that Hay and Nopcsa were correct in associating *Troödon* with the carnivorous dinosaurs.

Through the courtesy of Mr. L. Sternberg of the Royal Ontario Museum, Toronto, the writer received casts of the teeth of the University of Alberta specimen described by Gilmore (1924). A study of these together with Gilmore's illustrations and the illustrations by Brown and Schlaikjer (1943, p. 40) provided a good understanding of the teeth of the dome-headed dinosaurs.

They consist of a subcylindrical root, capped by a laterally compressed crown, which has a cingulumlike base. Both internal and external faces are vertically ribbed, and in the premaxillary teeth this ribbing extends from the edge of the tooth to the cingulum. Denticulations on the edges of the premaxillary teeth are only faintly defined. A well-pronounced "heel" is developed on the posterior edge. Maxillary and dentary teeth are less pointed than those of the premaxillae, but the denticles are very much more pronounced. These denticles merge into well-defined flutings on both faces of the crown, and in some cases extend from the edge of the tooth nearly to the base of the crown. In this respect the maxillary and dentary teeth resemble those of *Thescelosaurus* (Sternberg, 1940, figs. 1–8), but the flutings are not so extensive. Wear is always on the anterior and posterior edges, except where the crown is nearly worn down, and never shows as a long slicing cut on the center of the face.

From the above discussion, it is evident that *Troödon* was not a dome-headed dinosaur and that Gilmore was in error in regarding *Troödon* and *Stegoceras* as synonymous. Lambe's generic name *Stegoceras* must, therefore, be revived for the reception of the Belly River dome-headed dinosaurs.

Nor should the family name Troödontidae be used any longer for the dome-headed dinosaurs even though the characters given by Gilmore were those of the dome-headed forms. Troödontidae must be reserved for the family to which *Troödon* belongs, and recharacterization of this family will be necessary.

It is evident that *Stegoceras* was the first generic name proposed for a dome-headed dinosaur, but as Brown and Schlaikjer's generic name *Pachycephalosaurus* is much more descriptive of the family than Lambe's name *Stegoceras*, the writer proposes the new family name Pachycephalosauridae for the reception of the dome-headed dinosaurs. At present this family will include the genera *Stegoceras* and *Pachycephalosaurus*.

It is quite possible that when more is known about this group, it may be elevated to higher than family rank. In no other ornithopod do we find abdominal ribs or tongue and groove articulation on the zygapophyses.

In defining the new family the same characters given by Gilmore (1924, p. 8) for the Troödontidae are used with additions shown in parentheses.

Order ORNITHISCHIA
Suborder ORNITHOPODA
Family PACHYCEPHALOSAURIDAE, n. fam.

Family characters: Abdominal cuirass of segmented ribs; premaxillae with (or without) teeth; teeth in a single row (faces of crowns vertically ribbed, edges denticulate, base expanded); domelike thickening of parietal and frontal bones (occipetal condyle strongly deflected, neck probably

strongly arched as in the Hadrosauridae); dorsal vertebrae having zygapophyses with tongue and groove articulation; pelvic bones resembling the Ceratopsia in the horizontal widening of the preacetabular portion of the ilium and ischium without obturator process and with an elongated pubic process.

Genus STEGOCERAS Lambe

LAMBE, L. M., 1902, Canada Geol. Survey Contr. Canadian Paleontology, vol. 3, pt. 2, art. 2, pp. 68–69, figs. 1, 2, pl. 21.
LAMBE, L. M., 1918, Royal Soc. Canada Trans., ser. 3, vol. 12, sec. 4, pp. 23–36, pls. 1, 2.
GILMORE, C. W., 1924, Alberta Univ. Dept. Geology Bull. 1, pp. 1–43, pls. 1–15.
BROWN, B., and SCHLAIKJER, E. M., 1943, Am. Mus. Nat. History Bull., vol. 82, art. 5, pp. 121–148, pls. 33, 34, 43 and 44.

Genotype, *Stegoceras validus* Lambe.

Generic characters (emended): Small to medium-sized; thickness and position of dome variable; face short; skull more or less ornamented; premaxillae with teeth; premaxillary teeth pointed, with trenchant edges, faint marginal denticulations, faces of crown ribbed, posterior "heel"; maxillary and dentary teeth with well-pronounced denticulations extending onto both faces as flutings; supratemporal fossa nearly or quite closed; infratemporal fossa much reduced; premaxilla nearly excluded from lateral view; fore limb much reduced; four digits in the pes, first reduced.

STEGOCERAS VALIDUS Lambe

Holotype, G.S.C. no. 515, well-preserved frontoparietal mass from the Oldman (Belly River) formation, east side of Red Deer River, below mouth of Berry Creek, Alberta.

Plesiotypes, G.S.C. nos. 138, 1108, 8816 and Univ. of Alberta no. 2, from same general locality and horizon as the type.

Specific characters: Moderate-sized; frontoparietal mass relatively narrow and long; dome thick, well forward; frontals narrow anteriorly; parietals and squamosals forming horizontal shelf overhanging occiput; face moderately steep.

This species has been so fully described and figured by Lambe (1918), Gilmore (1924), and Brown and Schlaikjer (1943) that it need not be discussed further.

STEGOCERAS BREVIS Lambe

LAMBE, L. M., Royal Soc. Canada Trans., ser. 3, vol. 12, sec. 4, pp. 23–36 (1918).

Holotype, G.S.C. no. 1423, a well preserved frontoparietal mass from the Oldman (Belly River) formation, Red Deer River, below mouth of Barry Creek, Alberta.

Plesiotypes, G.S.C. nos. 121, 193, 194, 8819, from the same general horizon and locality as the type.

Specific characters (emended): Small form; frontoparietal mass short; dome only moderately thick, relatively far back; parietals strongly down-turned posteriorly; no horizontal shelf over occiput; dome smooth on top, pitted externally; frontals very broad and low anteriorly; face relatively flat; orbits in advance of dome.

Remarks.—This species has been well illustrated by Lambe (1902, figs. 3–5, the type), Gilmore (1924, pl. 8, figs. 1, 2, specimens in Univ. of Alberta), and Brown and Schlaikjer (1943, pl. 35, figs. 1–6, G.S.C. nos. 121 and 8819). It is unnecessary, therefore, to refigure any one of the specimens here.

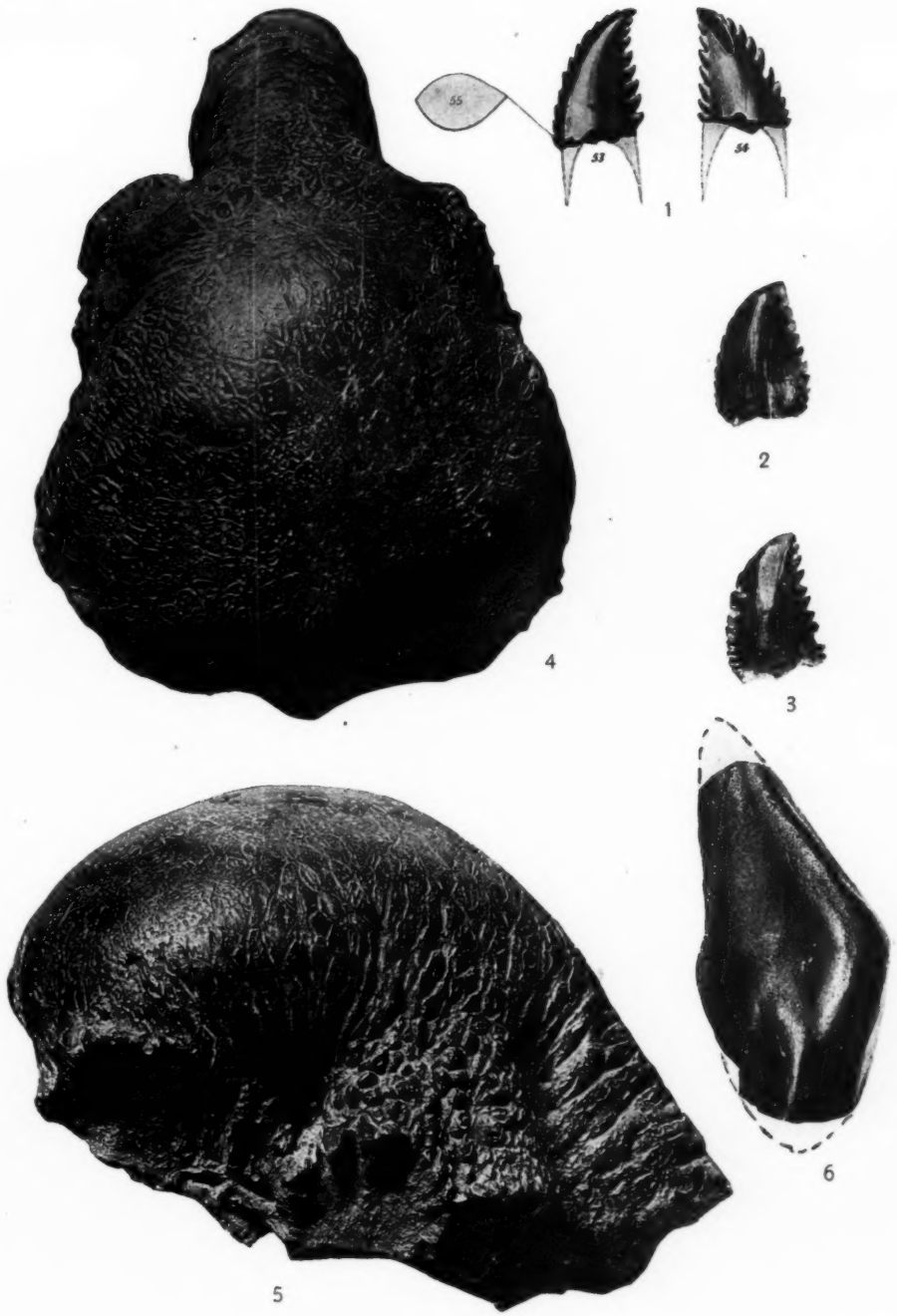
Brown and Schlaikjer do not recognize Lambe's *S. brevis*, but they believe that the differences are due to age and sex. They state that in all of the small skull roofs the sutures are quite open, that the increase in the height of the dome accompanies increase in size and, with the upgrowth of the frontoparietal area with age, there is a reduction of the posterior shelf. Careful examination of all of our specimens does not bear this out in every detail.

EXPLANATION OF PLATE 70

FIGS. *1–3—Troödon formosus* Leidy. *1*, Type, ×3, after Leidy. *2*, Maxillary? tooth G.S.C. no. 1267, external view, ×3. *3*, Maxillary? tooth G.S.C. no. 8841, internal view, ×3. (p. 534)

4, 5—Stegoceras lambei Sternberg, n. sp. Holotype, G.S.C. no. 8818, superior and lateral view, ×1. (p. 537)

6—Sandalodus liardensis Sternberg, n. sp. Holotype, G.S.C. no. 8847, superior view, ×2. (p. 539)



Sternberg, Dome-headed Dinosaurs

Of the five specimens of *S. brevis*, only the type (no. 1423), and no. 193 show open sutures, and even in these the bones are not separated. In nos. 121 and 194 the sutures on the roof of the endocranial cavity are only faintly shown and in no. 8819 the sutures cannot be detected, suggesting a mature individual. These are all relatively small. On the other hand, in a specimen of *S. validus*, (G.S.C. no. 2379) the dome is as thick as that of the type of *S. validus* and thicker than any specimen of *S. brevis*, yet the sutures between the frontals and between these bones and the parietals are open throughout their thickness, and the bones can be separated. Specimen no. 1549 represents the fused parietals with a well-pronounced horizontal shelf, and the dome is very thick, yet the suture was open. In all specimens of *S. brevis* the parietals are sharply down-turned, and in all specimens of *S. validus*, whether young or old, the parietals extend backward to form a horizontal shelf or crest over the occiput. The posterior development of the dome and the down-turning of the parietals are carried to extreme in G.S.C. no. 8818, to be described as the type of a new species, and the Lance *Pachycephalosaurus*. The thin broad frontals and the forward position of the orbits are well shown in all specimens of *S. brevis*. In the smoothness of the dome *S. brevis* resembles *S. edmontonensis* (Brown and Schlaikjer).

The above-mentioned characters must not be regarded as due to age or sex only, and Lambe was quite justified in establishing the species *S. brevis*. Except for the great difference in size. *S. brevis* is closer to *S. sternbergi* (Brown and Schlaikjer) than to *S. validus*. These very small and large forms resemble each other in the relative shortness of the frontoparietal mass, lack of posterior shelf, broad low frontals where they meet the nasals, and the smooth central portion of the dome. It would appear, however, that the two forms represent distinct species.

STEGOCERAS LAMBEI[1] Sternberg, n. sp.
Plate 70, figures 4, 5

Holotype, G.S.C. no. 8818, well-preserved frontoparietal mass, from the Oldman formation, South Saskatchewan River, 3 miles below Bow Island ferry, Alberta. Collected by the late E. J. Whittaker in 1923. This is the only specimen reported from this locality.

Specific characters: Relatively large form; skull short; face narrow and very steeply inclined; frontoparietal mass very thick, broad posteriorly and very narrow anteriorly; dome far back and overhanging occiput; no posterior shelf; posterior border steeply inclined.

Remarks.—Brown and Schlaikjer (1943, pl. 35, figs. 7–9) examined this specimen and figured it as *Troödon validus*. They regarded its differences as due to age. Yet this specimen differs from the type of *S. validus* more distinctly than does any other specimen which is referred to the genus.

The frontoparietal mass is thicker than in any other member of the family when compared to the length of the skull. It is very broad posteriorly and extremely narrow where the frontals unite with the nasals. There was no horizontal parietosquamosal shelf as in *S. validus*, but like *Pachycephalosaurus grangeri* the dome was pushed far back and overhung the occipital region.

Though the postorbitals and postfrontals are not present, the sutures for contact with these bones are so far down on the side of the cranium and so small, relatively, as to suggest that there was little or no shelf behind the orbits. A well-defined groove runs down the side of the face and separates the narrow part of the frontal that articulates with the nasal from that part of the frontal that overhangs the orbit. Just in front of the bulbous part of the dome another groove runs down the side of the head and separates the postfrontal and postorbital to within 10 mm. of the level of the orbit. It seems that the skull was pinched both in front of, and behind the orbit, and that the only overhang was above the bulging orbits. This was very different from the condition prevailing in *S. validus* as shown by Lambe (1918) and Gilmore (1924).

The suture for contact with the alisphenoid is a well-defined groove running from the external edge of the endocranial cavity to near the middle of the orbit, then turning sharply backwards to meet the narrow anterointernal edge of the postorbital.

The very narrow, steeply inclined frontals show that the head was short and that the

[1] Named in honor of the late L. M. Lambe.

face was very narrow and steep. The dome is about the same length as that of the University of Alberta specimen, described by Gilmore (1924) but is thicker, and the complete skull probably was much shorter. The braincase was relatively short. The total length of the frontoparietal mass is only slightly greater than in Lambe's type (G.S.C. no. 515) but in all other respects it is very much larger.

COMPARATIVE MEASUREMENTS
(Millimeters)

	Type of *S. lambei*	Type of *S. validus*
Length of frontoparietal mass between horizontal lines	120	105
Length of frontoparietal mass measured on inferior edge	100	95
Thickness of dome above endocranial cavity	74	37
Greatest breadth of dome	88	58
Breadth of dome directly behind orbits	65	58
Center of orbits to posterior edge of frontoparietal mass	74	75
Center of orbits to nasal contact	47	32
Median thickness of frontals at nasal contact	27	16
Greatest breadth of endocranial roof	22	16
Greatest length of endocranial roof	66	59

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JOURNAL OF PALEONTOLOGY, VOL. 19, NO. 5, PP. 539–540, SEPTEMBER 1945

A NEW SPECIES OF SELACHIAN FROM THE LOWER CARBONIFEROUS OF CANADA

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MANY genera and species of the Palaeozoic selachian suborder Bradyodonti have been described from the Mississippi Valley and other parts of the United States (Branson and Mehl, 1938; Newberry, 1889; Newberry and Worthen, 1866), but *Helodus subtuberatus* Lambe (1913) is the only species so far recorded from Canada. During 1944, Mr. C. O. Hage, of the Geological Survey of Canada, collected the enamel crown of a selachian tooth from the Liard Range, Northwest Territories.

Teeth of these fish are so variable that it is quite probable that several of the types described as distinct species eventually may be shown to belong to one species. Because of this and the fact that so many species have been described from Lower Carboniferous beds, one hesitates to establish a new species on a single tooth, but our specimen is quite distinct from anything described, and the locality is nearly 2000 miles from the localities where most of the specimens have been collected. Our specimen appears to most nearly resemble specimens that have been referred to *Sandalodus* (Newberry, 1889, pl. 21, figs. 6–8) and is here referred to that genus.

SANDALODUS LIARDENSIS Sternberg, n. sp.
Plate 70, figure 6

Holotype, the enamel crown of a large tooth, G.S.C. no. 8847, from the Mississippian of Liard Range, about 18 miles north of Fort Liard, Northwest Territories.

The specimen is tentatively identified as a left maxillary tooth. The greatest diameter is regarded as internal-external and the thicker edges anterior and anterointernal. Both tips and most of the edges were injured in collecting, but there does not appear to be much missing from any part except the ends. The tooth is roughly diamond-shaped, with the lingual part longer and narrower. It is moderately arched anteroposteriorly but almost flat internoexternally. The flatness is not the result of wear.

The crown is composed largely of tubular dentine, but the tubes do not quite reach the base of the enamel. The surface is shiny and covered with very fine punctae. Over most of the surface the distance between the punctae is greater than their diameter, but near the posterointernal edge the diameters of the punctae increase and are greater than the spaces between them. The punctae are not confluent as in *Sandalodus minor* Bryant (1936). On some parts of the crown the punctae are in irregular rows that run roughly at right angles to the longer diameter, but in other parts there is no definite arrangement.

External to the widest part of the tooth the median part of the crown tapers off into a sharp ridge, and the sides, especially the anterior, drop off rapidly. About halfway down this anterior face a low but sharp ridge forms the upper edge of a perpendicular face that extends to the lower edge of the crown. The posterior face slopes more gradually, and there is a slight rolling of the edge. Internal to the widest part the anterior face is thick and truncated and apparently fitted against the thick edge of another tooth. The posterior face of this part of the crown descends more gently and is only about half as thick as the anterior edge. The lower part of this edge is slightly roughened and appears to have been overlapped by another tooth.

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PALEONTOLOGICAL NOTES

PARROSAURUS, N. NAME, REPLACING NEOSAURUS GILMORE, 1945

CHARLES W. GILMORE
United States National Museum, Washington, D. C.

Dr. A. S. Romer has kindly called my attention to the fact that *Neosaurus* Gilmore, 1945 (JOUR. PALEONTOLOGY, vol. 19, no. 1, p. 25), is preoccupied by *Neosaurus* Nopcsa, 1923 (Fortschr. Geologie u. Palaeontologie, Heft 2, p. 53), and I therefore propose the new name *Parrosaurus* to take its place. *N. missouriensis* Gilmore, the genotype, therefore, becomes *Parrosaurus missouriensis* (Gilmore).

ILLUSTRATED CATALOGUE OF NORTH AMERICAN DEVONIAN FOSSILS

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JOURNAL OF PALEONTOLOGY, VOL. 19, NO. 5, PP. 541–543, SEPTEMBER 1945

REVIEWS

THE STRATIGRAPHY OF SOME LOWER ORDOVICIAN FORMATIONS OF THE OZARK UPLIFT, by James S. Cullison, Missouri Univ., School of Mines and Metallurgy, Tech. Ser. Bull., vol. 15, no. 2, pp. 1–112, pls. 1–35, Rolla, Missouri, June, 1944.

This commendable publication, the result of the author's studies since 1931, describes the stratigraphy and faunas of the principally dolomitic rocks of the Jefferson City group, and the Cotter, and Powell formations of parts of Missouri and Arkansas. It will be welcomed by geologists interested in the stratigraphy of the Lower Ordovician and in the "Ozarkian-Canadian" problem.

The larger and more important part of the paper is devoted to the author's revised Jefferson City group, which constitutes the lower half of the total maximum thickness of almost 1100 feet of rocks described and includes two-thirds of the 70 figured species. The Jefferson City group of Cullison is essentially the same as the Jefferson City formation of previous recent authors, and Cullison's placement of the lower boundary is not significantly different from general usage; the upper boundary, however, is revised upward. Cullison's placement of this upper boundary departs from the original usage of Winslow, whose Jefferson City formation included beds up to the base of the St. Peter sandstone, and from the more recent usage of the Missouri Geological Survey and others, who have followed Dr. E. O. Ulrich's unpublished recommendations in recognizing the base of the Hercules Tower sandstone of Cullison (so-called Swan Creek sandstone of local usage) as the boundary between the Jefferson City and Cotter formations. The upper boundary of the revised Jefferson City group falls at the base of an unnamed sand about 240 feet above the Hercules Tower sandstone. By this shift the Jefferson City group becomes essentially the zone of the gastropod genus *Orospira* with three faunally homogeneous subunits (see Cullison's pl. 2).

It is proposed by Cullison that the rocks included in his revised Jefferson City group be assigned to two new formations; the Rich Fountain, to include the lower third, and the Theodosia, with the Lutie and Blackjack Knob members (both new) for the remainder. In addition, field names are applied to a number of the beds or zones found to be helpful in correlation within the various formations. The descriptions of the new stratigraphic units, as well as those of the Cotter formation (maximum total thickness 340 feet) and Powell formation (observed incomplete thickness 214 feet), follow conventional patterns. Type sections are designated and described for all named formations and numerous supplementary sections are described. Locations of measured sections are given on a small-scale areal index map adapted from the state geologic maps of Missouri and Arkansas. The sections described are mounted on individual strips, which facilitates comparison.

The salient features of Cullison's report are summarized in a composite section and faunal distribution chart (pl. 2). The statistics of this chart are essentially as follows:

Formation	Restricted genera	Longer-ranged genera	Restricted species	Longer-ranged species
Powell	0	8	9	1
Cotter	2	7	10	2
Theodosia	3	9	24	3
Rich Fountain	6	9	23	2

A total of 67 named and three unnamed species are illustrated on plates 24 to 35, and 54 of the specific names are new. These are included in 31 named genera, seven of which are new, and one unnamed genus. Gastropods and trilobites are richest in numbers of species represented, with 21 each (excluding "species" of *Cerotopea*); whereas cephalopods, "species" of *Ceratopea*, brachiopods, and sponges follow in the order of decreasing numbers. All the illustrated and listed forms are described except one (*Hystricurus* cf. *H. conicus* Billings), and for the most part the illustrations and descriptions are adequate. With the exception of plates 26 and 27, the fulltone plates of fossil illustrations are very good, and the individual figures are in pleasing contrast with a black background. Plate 31, which illustrates the six "species" of *Ceratopea*, furnishes excellent illustrations

showing the variety to be found in this interesting gastropod operculum.

Critical appraisal reveals some defects. Although the collotype plates of fossils are generally excellent many of the half-tone plates of outcrops and rock types are so poor as to have little meaning, and the author neglected to provide a scale for most of them. Failure carefully to systematize the headings in the table of contents as well as in the text could lead the casual reader to wrong assumptions as to what formations the Jefferson City group contains. The described sections show a lack of careful editing and systematizing, especially noticeable with regard to the spelling of words properly ending in *eous*. Member and zone names are not given in the described sections, and even from the description in the text the reviewer could not be certain what the exact limits of the Lutie and Blackjack Knob members were intended to be in their type sections. The reviewer is chary of accepting the subspheroidal chert masses figured (pl. 5; also pl. 10 by reference to pl. 2) as "Cryptozoa-like" or even of organic origin, for similar stromatolitic masses show a surface of attachment which interrupts their continuity. References to Ulrich, Foerste, Miller, and Furnish are inconsistent in the text (pp. 65, 67), the plate legends (p. 103), and the bibliography (p. 110). The reference intended is to Special Paper 37 of the Geological Society of America, published in 1942. Identification of specimens from the faunal descriptions may be hampered by the paucity of comparative statements and the lack of profile views for some specimens. The report follows the outmoded reference of the Brachiopoda to a class of the phylum Molluscoidea, although it adopts the most recent subordinal revisions of the group. According to the advice of the author the name *Ceratopea calceoliformis* on plate 2 should be changed to read *C. jenkinensis*, and the spelling of the name *Lesueurilla* should be corrected throughout the paper.

Dr. Cullison has given stratigraphers an important report dealing with the difficult and sparingly fossiliferous early Paleozoic carbonate rocks of the Ozark region. Additional studies of the faunas of these rocks as true assemblages are needed for a really proper appraisal of the "systemic" boundary problems involved; and a more comprehensive discussion of the Jefferson City group may be expected when the Roubidoux formation has been studied in detail. It is to be hoped that it will be possible for the author to continue his work upward and downward from the strata discussed in his recent report.

PRESTON E. CLOUD, JR.

FOUNDATIONS OF PLANT GEOGRAPHY, by Stanley A. Cain, 556 pp., 63 illus., Harper & Brothers, 1944. $5.00.

A conservative estimate numbers the known living species of plants at 350,000 with new species being reported, during normal times, at the rate of about 4,800 a year. How many species comprised the evolving sequence of plants during geologic time will never be known because the fossil record is not a complete inventory. The description of living and fossil species and the notation of their geographical distribution are the activities usually included in plant geography. Dr. Cain's book, which he calls interpretive plant geography, is a philosophic treatment of the fundamental raw materials of plant geography which seeks to review and explain present theories of causes and processes governing the origin, association, dispersal, and extinction of species.

As may be surmised, a study of such scope entailed an extensive use of references and consultation with many living authorities. Viewed as a whole, the result is a book that has assembled into convenient form and has discussed competently the data from many diverse but related branches of botanical investigation. The Literature Cited section contains 720 selected entries pertaining to taxonomy, ecology, genetics, physiology, paleobotany, cytology, etc. Explanatory footnotes are scattered through the text and a glossary attempts to define most of the ecological, genetical and cytological jargon now probably understood only by the inner sanctum of initiates in those studies.

The book consists of five parts, each with a number of chapter subheads: 1. Introduction, which outlines the field the author intends to cover and restates the principles of plant geography. 2. Paleoecology, which reviews the methods and results of paleobotanical research and includes a special

chapter devoted to pollen analysis. 3. Areography, which deals with age and area, dispersal, endemics, senescence, and related topics. (This usage of the word areography, as though derived from the Latin *area*, is incorrect, for the word has already been preempted to mean a description of the surface of the planet Mars and is derived from the Greek *Ares*, Mars.) 4. Evolution and Plant Geography, which discusses the nature and evolution of species. 5. Significance of Polyploidy in Plant Geography, which deals with cytological and genetical studies. Nearly all chapters begin with concise summaries in italics.

As a paleobotanist I read the chapters on Paleoecology with particular interest. These contain well-chosen and adequately elaborated examples of the methods employed by students of fossil plants in formulating concepts of past climates, associations, and environments. Although in my opinion Dr. Cain accepts too many paleobotanical statements without benefit of the customary grains of salt, he is, nevertheless, aware that pitfalls exist. For instance, on page 36 he says, "The paleoecological method . . . requires extreme care in the identification of fossils and their reference to modern types. This is the greatest single source of error and limitation of the method." Thus, a number of the examples he cites will have to be amended somewhat because reexamination of many of the pertinent fossils shows that they have been misidentified, requiring, obviously, a new set of modern equivalents.

In spots the book is not easy reading, even with the help of the glossary, and many paragraphs would be much clearer if some ecological and nomenclatorial obfuscations had been rephrased in simpler terms. Perhaps some of these passages were not submitted to the acid test so felicitously referred to in the last paragraph (p. XIV) of Acknowledgments. A few words like floristic, organization, and mechanism, recur far too often throughout the book to retain their pungency. Ecological studies, in some quarters at least, appear to require for their expression a voluminous, involved, repetitious, and obscure phraseology. I doubt that this condition is necessarily inherent in or consequent to such studies but suspect that it develops from the faulty mental digestion of the practitioners. Dr. Cain's diagnosis is worded a little differently (p. 211): "In many instances the assumptions arising from deductive reasoning have so thoroughly permeated the science of [plant] geography and have so long been a part of its warp and woof that students of the field can distinguish fact from fiction only with difficulty." What plant geographers and ecologists therefore need is apparently not more words but more penetrating critics and more editors with constructive blue pencils.

ROLAND W. BROWN
Geological Survey
U. S. Dept. Interior

JOURNAL OF PALEONTOLOGY, VOL. 19, NO. 5, p. 544, SEPTEMBER 1945

SOCIETY RECORDS AND ACTIVITIES

CONTRIBUTIONS BY AMERICAN PALEONTOLOGISTS TO THE INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

On June 21, 1945, a check in the amount of $378.50 was sent to Mr. Francis Hemming, Secretary of the International Commission on Zoological Nomenclature, which is the sum realized from voluntary subscriptions by members and fellows of the Paleontological Society in support of the work of the Commission. The following letter, dated July 8, has been received in acknowledgment:

The Secretary,
The Paleontological Society,

Dear Sir,

When, as Secretary to the International Commission on Zoological Nomenclature, I recently received from the Treasurer of the Paleontological Society a cheque for the sum of $378.50 (£93.12s.7d), representing donations to the funds of the International Commission contributed by individual members of the Society, I at once reported to the members of the Executive Committee of the Commission the receipt of this important and most welcome gift to the funds of the Commission.

I now write, on behalf of the Executive Committee, to express the hope that you will be so good as to convey the grateful thanks of the International Commission both to the Council of the Paleontological Society for having organised the collection of this fund and to the members of the Society for having so generously contributed thereto.

It is the constant aim of the International Commission to discharge the duties entrusted to them in the manner best calculated to promote the orderly development of zoological nomenclature. In order, however, that the International Commission may be in a position to render to zoologists the best service in their power, it is essential that the Commission should be possessed of sufficient funds to enable them at all times to deal promptly and efficiently with cases submitted to them for consideration. It is therefore particularly gratifying to the International Commission and a great encouragement to them in their work, when a leading scientific society such as the Paleontological Society gives corporate expression to the value which it attaches to the work of the Commission and, by raising a fund to augment the financial resources of the Commission, gives help of the most practical kind in the direction where such help is most needed.

Very truly yours,
FRANCIS HEMMING
Secretary to the International Commission on Zoological Nomenclature

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"I can make a better Microscope"

Professor Gilman was startled by the statement of his guest, Charles A. Spencer. He had been exhibiting his prize possession—a microscope made by Chevalier of Paris.

That was in the fall of 1846. Often during the following months, Dr. Gilman, a professor in the College of Physicians and Surgeons, New York, amused his friends with the story of the presumptuous backwoodsman who challenged the leading optician of France.

Six months later Spencer presented two objectives to the Professor.

Gilman placed them on his microscope and studied specimen after specimen. At last, bursting with excitement, he gave his verdict: "Why these are excellent! How did you do it?"

Charles Spencer took home to Canastota, New York, the first order ever given to an American for the manufacture of a microscope.

In another six months (October, 1847) the microscope was completed. On his way to deliver it, Spencer stopped at West Point to have the instrument tested by Professor J. W. Bailey, "father of microscopic research in America." Bailey was enthusiastic, acclaimed it "decidedly superior to Chevalier's," and added that it was at least equal to the Lowell instrument at Boston.

Thus Charles A. Spencer, self-taught and with only the experience gained in his homemade workshop, took his place beside the most experienced opticians of Europe.

Today, nearly a century later, the name Spencer is the hallmark of highest quality in scientific instruments. Research insures the perpetuation of the Spencer ideal.

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